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ARTICLE 1

THREE NEW SPECIES OF TRICHOPTERA FROM WESTERN PENNSYLVANIA

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JOHN S. WEAVER III¹

ABSTRACT

This study deals with three new species of Trichoptera from Powdermill Nature Reserve of Carnegie Museum of Natural History located in Westmoreland Co., Pennsylvania. The adult forms of *Stactobiella solzhenitsyni*, new species (♂), and *Neophylax wigginsi*, new species (♂, ♀), as well as adult, larval, and pupal stages of *Apatania blacki*, new species, are described and discussed.

INTRODUCTION

Two years of intensive collecting of western Pennsylvania Trichoptera have resulted in the discovery of three new species belonging to the following genera: *Stactobiella*; *Apatania*; *Neophylax*. *Stactobiella* and *Apatania* are holarctic in distribution with species occurring in the temperate regions of Europe, Asia, and North America. *Neophylax* species are confined to North America and Asia, most of the known species occurring on the former continent.

Collections of adults were made with light-traps and sweeping nets. Larvae and pupae were either picked by hand or were collected with a cylindrical, quantitative sampler (Hess type). The number of Trichoptera specimens collected in light-traps at Powdermill Nature Reserve were so numerous that it was virtually impossible to identify and separate all the collected material. Thus, future studies of existing material,

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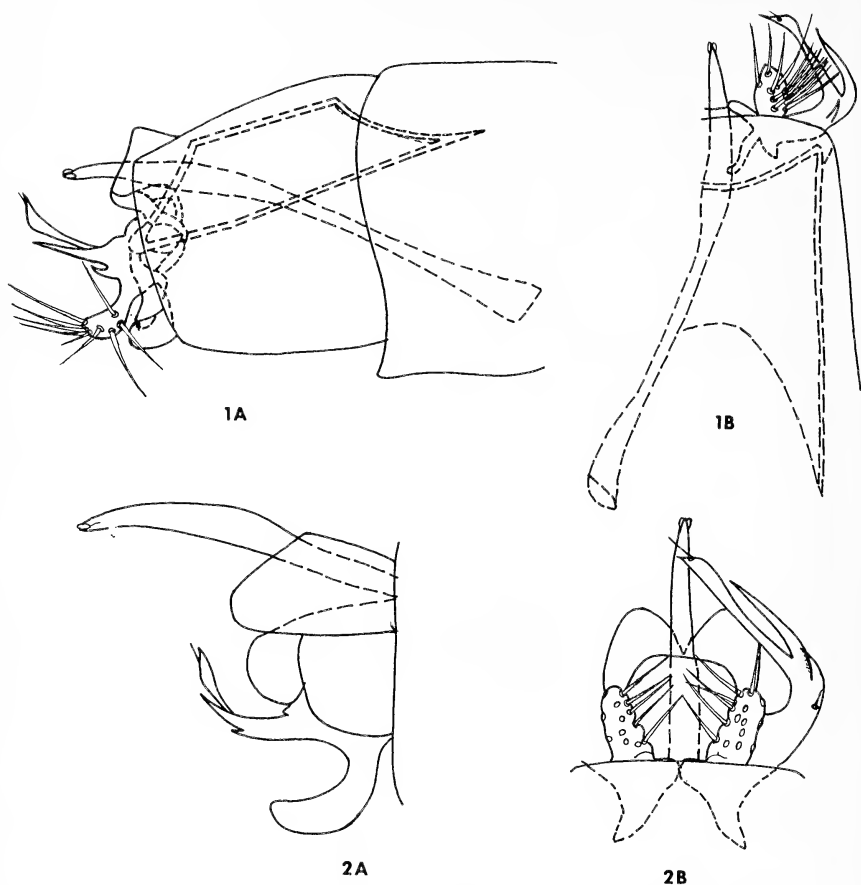


Fig. 1.—*Stactobiella solzhenitsyni*, new species, holotype, male genitalia. A, lateral view; B, ventral view.

Fig. 2.—*Stactobiella biramosa* Martynov (Angara River, Siberia); male genitalia. A, lateral view; B, ventral view.

as well as of any new collections from the same area may produce additional interesting species of Trichoptera.

SYSTEMATIC ACCOUNTS

Stactobiella solzhenitsyni, new species

This species from the family Hydroptilidae belongs to the group of *biramosa* Martynov. It has trifurcate bracteole (sensu Ross, 1948) with two long "fingers," one small hook-like projection near the base and

ovate claspers. The tenth tergite is very short, membranous, and truncate at apex.

Holotype.—Male; Whiteoak Run near Holland House, Powdermill Nature Reserve, Westmoreland County, Pennsylvania, 19–20 June 1976, obtained by Jan L. Sykora and John S. Weaver. Deposited in collection of Carnegie Museum of Natural History.

Paratypes.—33♂, same data as for holotype. One male in the National Museum of Natural History, Smithsonian Institution, the remainder in the senior author's collection.

Description

Male: Length 2.4 mm. Wings mottled with gray and black dots. Ocelli present. Palpi, head, thorax dark gray; abdomen and legs gray. Metascutellum as described by Ross (1944) for *Stactobiella palmata*. Male genitalia (Fig. 1): Eighth segment with very short mesoventral process; ninth segment long and tubular with deep incision in the middle of apicodorsal section, from which a very short membranous part of the tenth tergite arises, covering part of phallus. Tenth tergite ventrally supported by a crescent-shaped, chitinous structure. Remaining part of the tenth segment extended posteriorly into an internal frame, rhomboid from lateral view, with relatively short posteroventral corners. Claspers in ventral aspect ovate with slightly pointed tip and dilated lateroapical section; in lateral view spoon-shaped with base attached to a large, triangular and sclerotized process directed ventromesally. Paired bracteole arising above claspers divided into two long, finger-like and pointed processes whose curved bases are elbow-shaped. Mesal "finger" one third longer than the lateral process, with dilated, arrow-shaped apex. From the base arises a short hook directed posteriorly and slightly dorsally. Aedeagus tubular, dilated shortly before apex, with a broad triangular base.

Discussion

The closest relative of *Stactobiella solzhenitsyni* is a Palaearctic species, *S. biramosa* Martynov, described from a tributary of the Ob River in Siberia. The bracteole of *biramosa* on Martynov's (1934) illustration shows only bidentate processes, a character accepted by Ross (1948) in his discussion of known species of *Stactobiella*. In the original description, however, Martynov (1934) clearly states that there is a third process, short and hooklike, arising near the base of the bidentate apex. The examination of a male collected along Angara River near Rasputina Taiga on 30 July 1926 (Fig. 2) supports Martynov's statement and reveals that the bracteole of the Siberian species *biramosa* Martynov, and of the North American *solzhenitsyni* are almost identical. These two species differ only in the ventral view of the claspers and the shape of the tenth tergite. The claspers are parallel-sided, almost quadrangular in *biramosa*, and ovate in *solzhenitsyni*; the tenth tergite is deeply divided in the former, very short and quadrangular in the latter. The Nearctic species *S. palmata* (Ross) is another close relative of *S. solzhenitsyni*, differing chiefly in the shape of the bracteole and claspers. According to Ross (1948) the genus *Stac-*

tobiella is formed by three component phylogenetic units. One of them is the *biramosa* group which is composed of the three closely related species mentioned above. Definite conclusions concerning the distribution of this group, however, cannot be made until more information on this new species is available.

Habits

The larva and the adult female of this species are not known. It is possible that the immature stages live in fast flowing, eurythermic streams such as Whiteoak Run, and not in mountain streams similar to Powdermill Run. Adults of another species, *Stactobiella delira* (Ross), were collected at the same locality (Holland House) during the previous month (May) as well as in June along Powdermill Run at a higher elevation. The flight period of *S. solzhenitsyni* seems to be limited to June, *S. delira* flying in May at the same locality.

Etymology

I take much pleasure in naming this species for Mr. Aleksander I. Solzhenitsyn, the great Russian author, who once shared the same country with the closest relative of the new species—*Stactobiella biramosa* Martynov.

Apatania blacki, new species

A detailed study of several springs in western Pennsylvania revealed a new species closely related to *A. rossi* (Morse) and *A. incerta* (Banks). In order to obtain data on quantitative and qualitative distribution of Trichoptera larvae, one of the localities, Maul Spring in Powdermill Nature Reserve, was sampled on a monthly basis resulting in the accumulation of a large quantity of *Apatania* immature stages. This plus the aforementioned collection of 1975–76 has made it possible to present description of adults, larvae, and pupae.

Holotype.—Male; Maul Spring, Powdermill Nature Reserve, Westmoreland County, Pennsylvania, 6 May 1975, obtained by Jan L. Sykora and John S. Weaver. Deposited in collection of Carnegie Museum of Natural History.

Paratypes.—1♂, same data as for holotype; 4♂ 5♀, same locality as for holotype, 31 May 1975; 1 ♀ same locality as for holotype, 19–20 June 1975; 1♀, Beck Spring, Forbes State Forest, Somerset County, Pennsylvania, 23 April 1976. One male and one female deposited in the National Museum of Natural History, Smithsonian Institution, the remaining specimens in the senior author's collection.

700 larvae and pupae: Maul Spring, Powdermill Nature Reserve, Westmoreland County, Pennsylvania, January 1975 through January

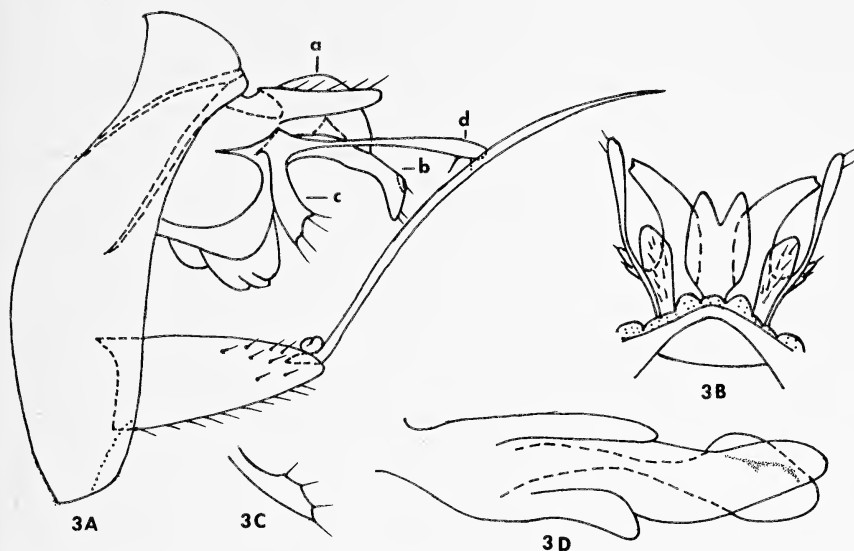


Fig. 3.—*Apatania blacki*, new species, holotype, male genitalia. A, lateral view; B, dorsal view; C, right ventrolateral process, lateral view; D, aedeagus, lateral view.

1976. 42 pupae (pharate adults): Beck Spring, Forbes State Forest, Somerset County, Pennsylvania, 23 April 1976.

Description

Apatania blacki is characterized by ventrally curved, long ventromesal process of the tenth segment and very long, slender apical segment of clasper.

Adults.—Male: Length from head to tip of wings 8.2 mm. General structure typical for the genus. Wing membrane dark brown; head, thorax, coxae and femora black; abdominal sclerites, tarsi, palpi and tibiae brown. Male genitalia (Fig. 3): Ninth segment a ring-shaped narrow strip of chitin, divided into a short and triangular "dorsal" and larger ventral sections. Tenth segment composed of several short branches.

Cerci long with truncate apex. Dorsomesal process of tenth tergite (a) short with closely fused lobes, similar to *A. prevolans* (Morse), forming a triangular incision; ventromesal process (b) curved sharply ventrally and laterally, with a slightly undulating ventral margin and rather sharp apex; dorsal part of the curved section with a heavy sclerotized patch bearing several setae; ventrolateral processes (c) variable, either scoop-shaped, gradually broadening towards the apex, bearing four setae, or (similar to those of *A. rossi*) with slightly clavate apices. Shape of tenth sclerite (Fig. 3C) varies considerably even between left and right side of one individual. Dorsolateral process (d) long and club-shaped. Claspers two-segmented, with the lateral aspect of the basal segment triangular; apical segment longer than in *A. rossi* and *incerta*, gradually curved along its length and with pointed apex bearing short spiculae. Phallus with a large, bulbous apex, and a long, broad lateral process.

Female terminalia (Fig. 4): Ninth and tenth segments very short. Ventral aspect of tenth segment with five very small, rounded lobes at posterior margin; posterolateral

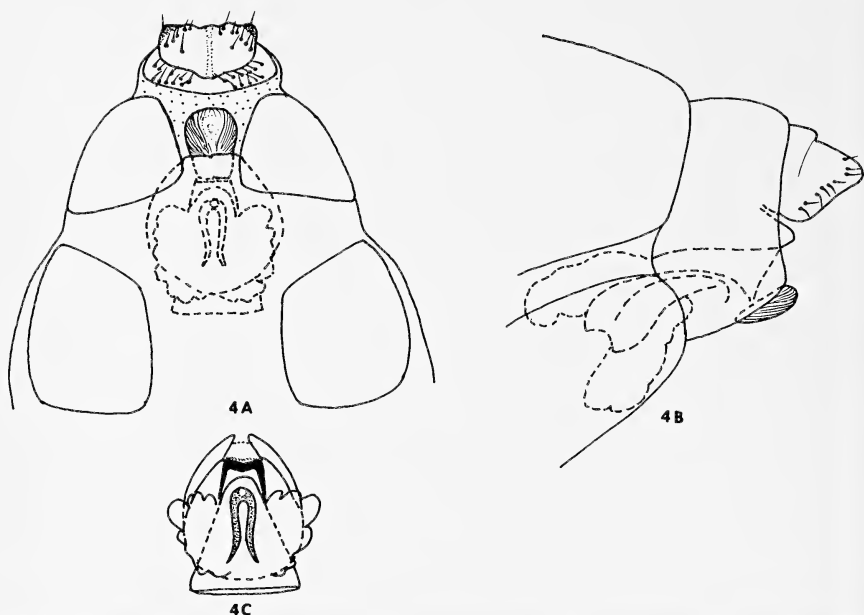


Fig. 4.—*Apatania blacki*, new species, female genitalia. A, ventral view; B, lateral view; C, bursa copulatrix, ventral view.

corners rounded, and more sclerotized than remainder of terminalia. Genital pocket trapezoidal of ninth segment, similar to *A. prevolans* (Morse). A heavily sclerotized, narrow semicircular area situated dorsally to genital pocket with two pairs of "wings" surrounding bursa copulatrix. Bursa is flask-shaped, with a round and bulbous posterior part, and a long, narrow anterior neck.

Immature Stages.—Larva (Fig. 5): Length of full-grown larvae 4.9 to 5.2 mm, case 6.0 to 6.2 mm. Head uniformly dark brown except yellow patches around both eyes with flat dorsum, rounded sides and the rear surface bearing short spiculae. Two prominent, black setae 14 and 15 (*sensu* Nielsen, 1942), arising even closer together than in *A. arizona* (Wiggins, 1973); the distance between their base is much less than one-half diameter of the eye. Labrum with anterolateral lobes covered with soft hairs; two pairs of primary setae present on dark sclerotized area are black, three posterolateral pairs are transparent. Anteromesal pair (*sensu* Nielsen, 1942) is evidently missing as in *A. arizona*. Labium with small labial palp, otherwise similar to that of *A. arizona*. Pronotum dark reddish brown, its posterior edge forming a dark ridge. Mesonotum with two reddish brown, large, rectangular sclerites. Metanotum with sclerite sa 1 (Nielsen, 1942) represented usually by 22 setae arranged in transverse row (Fig. 5A); sa 2 reduced, usually divided into two patches surrounded by five setae; sa 3 is typical, sickle-shaped sclerite with 10 setae. Mesosternum with 4 to 5 setae in middle; metasternum with mesal, round patch of 25 to 27 setae. Legs, similar to those of *A. arizona* with tarsal claw short, basal seta reaching almost to tip of claw, trochanter brush present on forelegs, absent from others. Dorsal hump on first abdominal segment lacking, dorsum covered with several rows of setae, ventral hump smaller than in *A. arizona* and covered with short, stiff hairs (approximately 130). Abdominal segments 2 and 3 dorsally with a pair of presegmental,

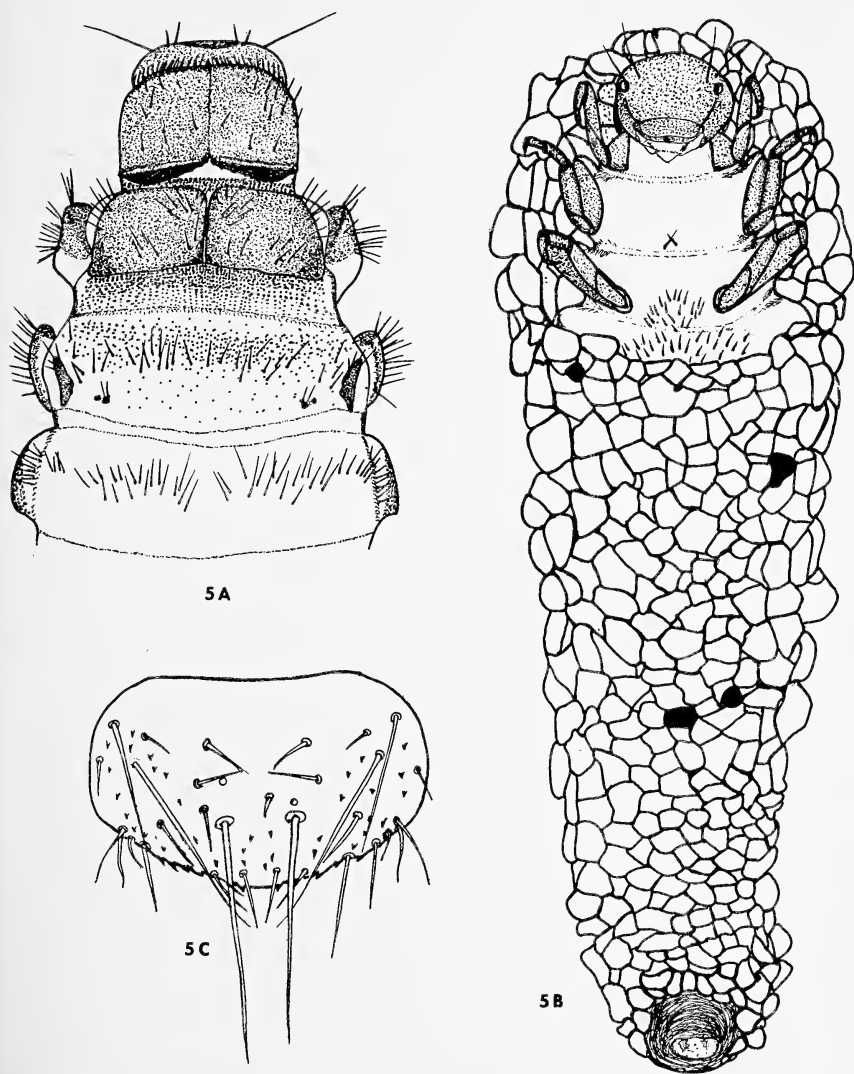


Fig. 5.—*Apatania blacki*, new species, larva. A, head and thorax, dorsal view; B, larva in the case, ventral view; C, dorsal sclerite of ninth segment.

single gill filaments, one pair of postsegmental gills present on dorsum of segment 2-4; ventral aspect of abdominal segments only with postsegmental pairs of gills on segment 2-4. Last abdominal segment with lateral sclerite sickle-shaped, bearing three long setae located dorsally, and with a single proleg hook (Fig. 5D). Ninth tergite (Fig. 5C) quadran-

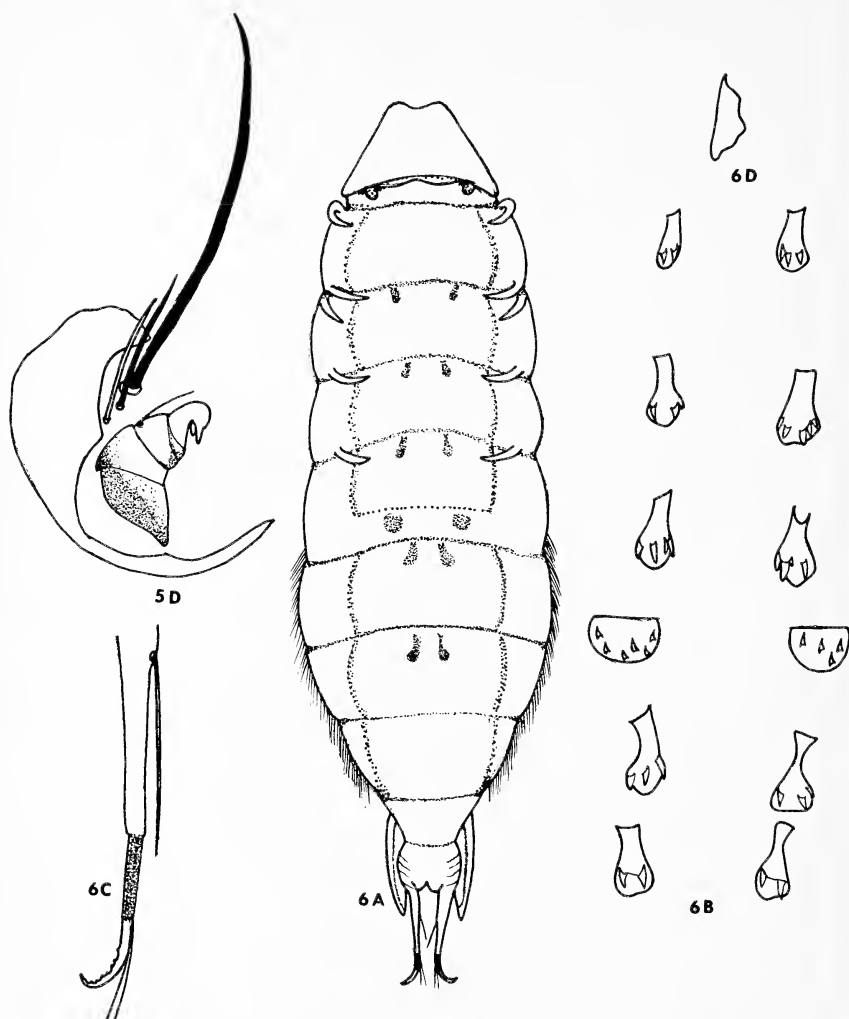


Fig. 5D.—*Apatania blacki*, new species, larva, prolegs with lateral sclerite, lateral view.

Fig. 6.—*Apatania blacki*, new species, pupa. A, abdomen; B, enlarged sclerotized dorsal plates; C, enlarged anal process; D, left mandible.

gular with rounded corners similar in shape to that of *A. incerta* (Flint, 1960). Case is cornucopia shaped, very smooth and built of small sand grains. Fourth and fifth instar larvae build the front section into a hood covering the head, which is less pronounced in younger instars. The same "curved hood" has been described by Wiggins for *A. arizona*. End of the case covered with silky membrane perforated with a round opening in the middle.

Table 1.—Gill data for pupa of *Apatania blacki*.

Segment	Dorsum		Ventrum	
	presegmental	postsegmental	presegmental	postsegmental
1	1 pair	1 pair	—	1 pair
2	1 pair	1 pair	—	1 pair
3	—	1 pair	—	1 pair
4	—	—	—	1 pair
5	—	—	—	1 pair

Pupa (Fig. 6): Length 6.0 to 6.2 mm, case 6.5 mm. Typical for the family and for the genus *Apatania* but may be distinguished from the remaining species by the anal processes in male specimens, shape and decoration of sclerotized plates on abdomen.

Labrum with ten long, hooked setae. Mandible with a short apical tooth and proximal cutting edge. Two setae in the middle of the face shorter than the pair of setae located on vertex between antennae. Abdomen with sclerotized plates as illustrated (Fig. 6B); five pairs with substantially dilated caudal parts, usually with three spines and narrow anterior sections. Anal processes with laterally serrate and curved apices and a median brown colored section bearing two setae. Another long seta located at the caudal end of the basal third of the anal process. Male pupa with typical lateral sheath covering the curved, apical segment of clasper (Fig. 6A). Data on gills are given in Table 1.

Anterior section of pupal case extended into a rounded hood which is attached to a stone surface with a silky membrane, that covers the opening on the ventral side.

Habits

The genus *Apatania* is distributed in streams and springs of the holarctic region. Most species are restricted to cold waters of the extreme north, or live in mountain springs and streams. Several very closely related species have been described from springs, suggesting a possible postglacial separation and distribution. In eastern United States, *Apatania* species belong to the *complexa* group, but form a distinct special *nigra* "subgroup" (Schmid, 1953), characterized by long, needle-like last segment of claspers and by short and broad dorsal processes. Until now only four species of the *nigra* complex have been described from eastern United States. They are *Apatania nigra* (Walker), *incerta* (Banks), *A. praevolans* (Morse), and *A. rossi* (Morse).

Larvae of *A. blacki* are found in cold spring brooks where the water temperature ranges between 8 to 10°C throughout the year. Because of this narrow ecological range they occur in fairly short reaches of springfed streams near the source where temperature variations are minimal. In Maul Spring area they inhabit the first 400 ft of the run-off stream, below this the *Apatania* larvae are scarce, and disappear at a distance of approximately 800 ft from the spring. The life cycle is similar to that of *A. incerta* (Flint, 1960). Larvae of *A. blacki*, however, hatch earlier, probably in May or June, the second instar larvae appearing early in July. Larval development is nearly complete by the begin-

ning of cold season, and most of the winter is spent as prepupae, the pupae occurring in late March through May. Adults are rather rare, apparently diurnal and are not particularly attracted to light.

Etymology

It is a great pleasure to name this species for Dr. Craig C. Black, the director of Carnegie Museum of Natural History, whose interest and assistance was essential for completion of this study.

Neophylax wigginsii, new species

This new species is closely related to *N. atlanta* Ross, differing chiefly in the lateral aspect of the tenth tergite, which is divided by a shallow incision into two very short lobes. The lateral view of the preanal appendage (*sensu* Schmid, 1955) is almost "parrotbeak"-shaped, with an extended and rounded dorsal portion. The clasper, closely attached to the ninth segment, is large with a posteriorly pointed dorsal projection and rounded ventral section.

Holotype.—Male; Maul Spring, Powdermill Nature Reserve, Westmoreland County, Pennsylvania, 10–11 September 1975, collected by Jan L. Sykora and John S. Weaver. Deposited in collection of Carnegie Museum of Natural History.

Paratypes.—11♂ 5♀, same data as for holotype; 1♂ 13♀, same locality as for holotype, 11–12 October 1975. One male and one female in the National Museum of Natural History, Smithsonian Institution, one male and one female in the Royal Ontario Museum, Toronto, Canada. The remaining specimens are in the senior author's collection.

Description

Male: Length 12 mm. Head, antennae, palpal, legs, and body generally brownish yellow. Abdominal tergites somewhat darker, genitalia brown. Front wing membrane uniformly gray, a large yellow area along the posterior margin not forming the typical double diamond shape as in *Neophylax concinnus* McLachlan. Another light yellow mark located near the apex along the margin surrounding the apical section of M2, and an oval and almost transparent area located near the tip of the wing between R5 and M1. Hind wings almost transparent, somewhat grayish and yellow in color. Male genitalia (Fig. 7): Seventh sternite with a ventral, spear-shaped projection. Ninth segment triangular in lateral view, the dorsal half reduced to a narrow, chitinous strap. Tenth tergite large, its apex divided by a shallow incision into two very short lobes with rounded apices of which the dorsal one is larger than the ventral. Preanal appendages large "parrothead"-shaped sclerites with rounded dorsal section, and ventrally pointed, sharp "beak." Clasper is a dark brown sclerite, located ventrally of the preanal appendage divided into terminal and basal segments. The terminal segment (Fig. 7A,a) large, approximately quadrangular with the posterodorsal corner extended into a short and sharp projection; posteroventral corner blunt, bent and extended mesally, forming a ribbon-shaped process. Basal section (Fig. 7A,b) of the clasper short and quadrangular in ventral view. Phallus with tubular base; its apex composed of long, pointed dorsal lobe and short, spear-shaped ventral part.

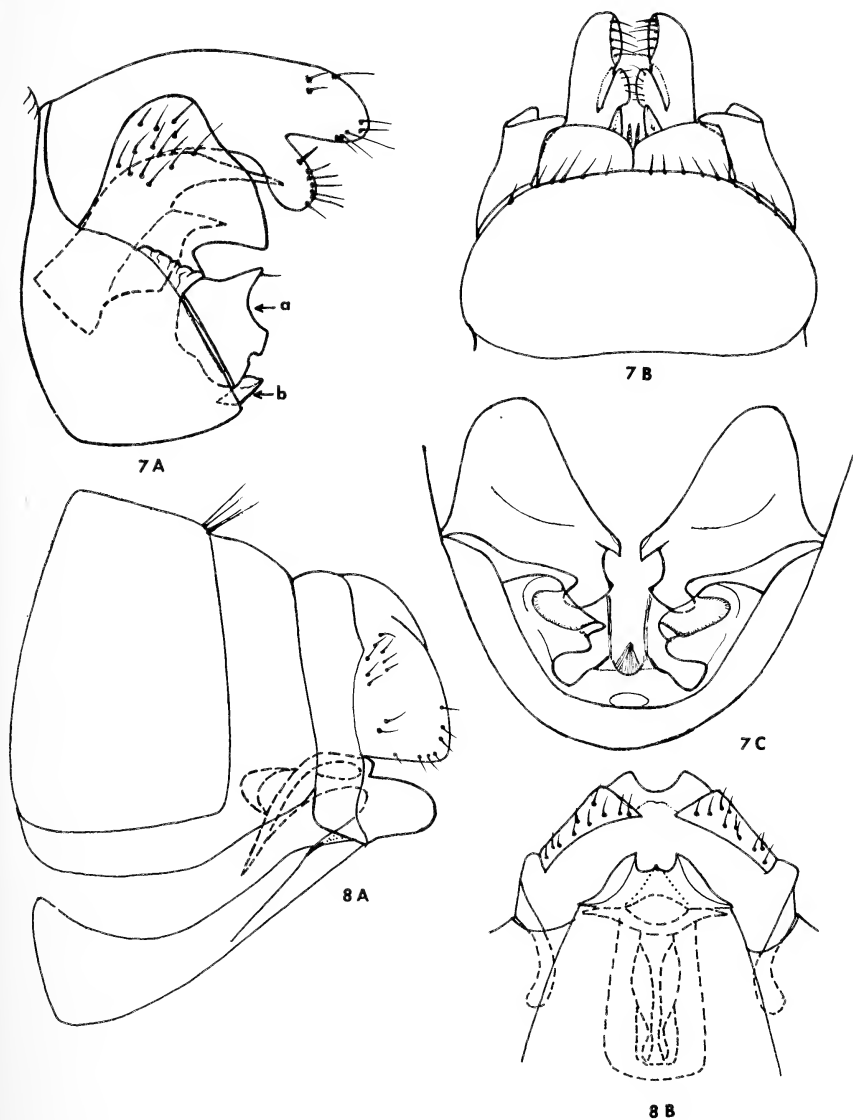


Fig. 7.—*Neophylax wigginsii*, new species, holotype, male genitalia. A, lateral view; B, ventral view; C, caudal view.

Fig. 8.—*Neophylax wigginsii*, new species, female genitalia. A, lateral view; B, ventral view.

Female (Fig. 8): Similar in coloration and habitus to the male. Subgenital plate strongly sclerotized with lateral corners extended into sharply pointed lobes, and bearing a short point in the middle. Subgenital plate is rounded at apex from lateral view. Ninth and tenth segments very short, tenth divided into two pairs of short triangular lobes. Ventral aspect of genital pocket lens-shaped; bursa copulatrix "bottle-shaped" with the narrow neck directed anteriorly.

Habits

Neophylax wigginsii is a rare species, the adults occurring in limited numbers around Maul Spring in September and October only. Inhabiting this spring and its runoff are three other species of *Neophylax*—*aniqua* Ross, *consimilis* Betten, and *ornatus* Banks. The occurrence of several adults of *N. concinnus* McLachlan in the light-traps was understandable as this species lives in the neighboring stream, Powdermill Run. The most common *Neophylax* species in the spring area is *N. aniqua*. Based on limited observation, it would appear that *N. wigginsii* lives in cold springbrooks or small mountain streams and the adults emerge in the autumn.

Etymology

It is my pleasure to name this species for Dr. Glenn B. Wiggins, Royal Ontario Museum, who confirmed our opinion of its being new.

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FLORAL VASCULAR ANATOMY OF *MEDEOLA VIRGINIANA* L. (LILIACEAE-PARIDEAE = TRILLIACEAE) AND TRIBAL NOTE

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ABSTRACT

The complete vascular floral anatomy of *Medeola virginiana* L. ("Indian cucumber") from its mid-pedicele to the recurved style-stigmas is presented. The lower pedicel contains a double ring of 12 (that is, six inner plus six outer) bundles. The six outer do not branch or fuse and directly establish the six tepal medians, three in an outer whorl and three in an inner whorl. The six inner bundles, which alternate with the six tepal median establishing bundles, are clearly compound, and following successive radial divisions and planar fusions establish the tepal laterals (both whorls), the stamen traces (both whorls), the three dorsals, the six dorsal laterals, the three ventral laterals, the six ventral placentals, and the three septal axials. The stamen, dorsal, ventral lateral, and septal axial traces are all fusion products. No septal glands or dorsal notches occur in this species, neither do raphides. The three inner, fused septal wings are completely free centrally at the gynoeceal base, hence this tricarpellate gynoeceum is unilocular. Three bundles (that is, continuing dorsal plus two branches from different ventral laterals) occur in each of the three recurved stylar arms. A stigmatoid support system composed of papilloid cells lines the inner notched stylar furrows and is continuous through the short, common, hollow stylar canal to the base of the gynoeceum along the inner septal wing margins.

INTRODUCTION

Medeola virginiana L. is a monotypic species of eastern North America (Fernald, 1950; Johnson, 1969) with a reported chromosome number of $2n = 14$ (Stewart and Bamford, 1942; Woodard, 1948). This report on the vascular floral anatomy of *M. virginiana* supplements the preliminary reports made by Anderson (1940) and Berg (1962a), and is part of a larger study of the baccate species of the Liliaceae Alliance

(Utech and Kawano, 1976a, 1976b, 1978). The manner of vascular presentation for *M. virginiana* will parallel that published for the other liliaceous species.

Historically, the berry fruit has been the major basis of taxonomic association of *Medeola* with *Trillium*, *Scoliopus*, and *Paris*. It is hoped that this investigation of the complete floral vascular anatomy of *Medeola* can be used directly in its tribal (or familial) assessment by establishing the vascular pattern underlying the berry fruit.

MATERIALS AND METHODS

For this vascular anatomical study, a series of floral buds through mature flowers of *M. virginiana* was collected over a month period from Laurel Hill State Park, Somerset Co., Pennsylvania (Utech, 76-201 CM) with fixation in acetic ethanol (1:3) and subsequent storage in 70% ethanol. Twenty-five flowers (buds to maturing fruits) were sectioned between 12–16 μ using standard paraffin techniques and stained in safranin and methylene blue (Sass, 1965; Johansen, 1950; Berlyn and Miksche, 1976). Checks on these serial preparations were made by observing whole flowers which had been cleared in 10% NaOH with the vasculature simultaneously stained in 1% fuchsin (Fuchs, 1963; Utech and Kawano, 1976a). Neither ontogenetic nor teleological implications are intended by the vascular description of the hypothetical ascent of the bundles from the pedicel to the stigma. Figs. 1–3 present photomicrographs of the pedicel to stigma vasculature, whereas Figs. 4–5 summarize the overall floral vasculature patterns. Text introduced coding is presented for the various bundle types.

Although the letters for the various vascular bundles are similar to those used in previous papers, a correspondence is given here between them and those used by Berg (1962a) for *M. virginiana*: D (dorsal) = m.s. (median carpellary strand); D_L (dorsal lateral) = s.s. (small strand); V_L (ventral lateral; compound) = l.s. (lateral strand; composite); vlb (ventral lateral branch) = l'.s (lateral strand; single, simple); Ventral Supply-SA (septal axials) + V_P (placentals) + F (funicular) vs. pl.s. (placental strand).

OBSERVATIONS

Pedicel Vascularization

In both the flowering and fruiting pedicel, the vascular bundle arrangement is exactly the same. Each pedicel in cross-section has a broad ring of 12 separate bundles that are clearly divisible into two groups, that is, six smaller bundles which are somewhat further from the center than the second set of six larger alternating bundles (Fig. 1A–C). The six smaller bundles represent the tepal medians (three outer tepal medians—OTM; three inner tepal medians—ITM). They depart from their outer pedicel position in two whorls to directly supply the three outer and three inner tepals, respectively. No fusion or cross-innervation occurs in their formation (Fig. 5). The six larger bundles (P), on the other hand, are responsible via repeated lateral division for the formation of the tepal laterals (TL) of both tepal whorls, and with additional division and cross-fusion for the total stamen, the dorsal and the ventral supplies (Figs. 4, 5).

Both in bud and early flower, the flowering pedicel is curved down-

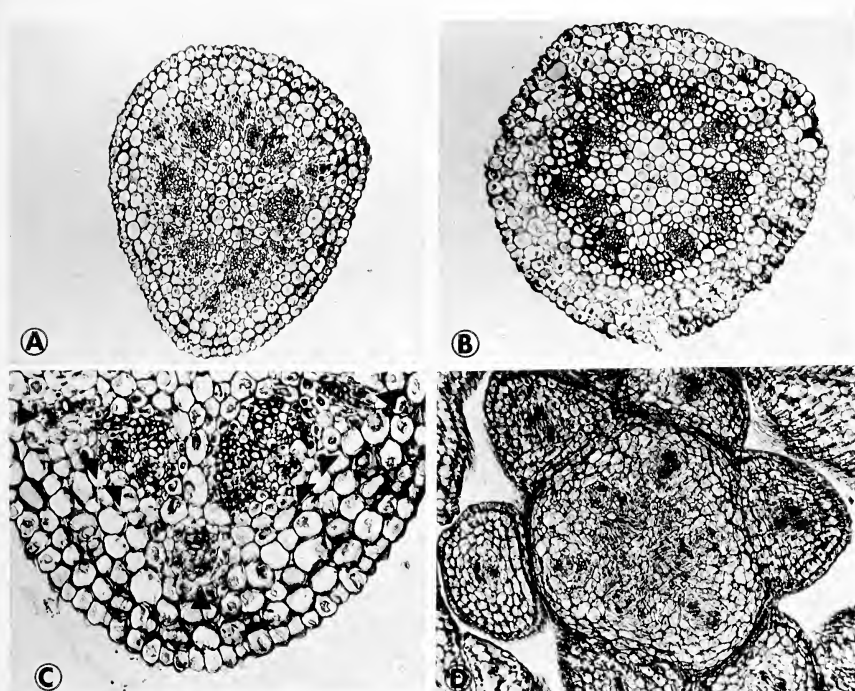


Fig. 1.—Vascularization of *Medeola virginiana*. A. Mid-length cross-section through a flowering pedicel showing the two sets of six bundles. The outer, smaller six depart directly to form the two whorl sets of tepal medians. The inner, larger six are compound and establish via repeated division the remaining floral vasculature (45 \times). B. Mid-length cross-section through a fruiting pedicel with a similar bundle arrangement as in A, but with the additional sclerenchymatous sheath around the bundles (45 \times). C. Enlargement of A showing three outer pedicel bundles (isosceles triangles) with two alternating inner compound bundles (paired equilateral triangles) (100 \times). D. Young bud cross-section showing bundle arrangement at the base of the receptacle. The two whorls of three stamens each are freed and their single fusion bundles lie along similar radii as the three dorsals and the three ventral laterals (40 \times).

wards below the upper whorl of leaves, and there is no sclerenchymatous sheath which encloses the 12 pedicel bundles. However, the fruiting pedicel which is erect and has undergone an upwards shift does have a sclerenchymatous sheath (Fig. 1B). It may be that the thickening of certain cell walls in this central zone (Fig. 1A–C) is directly related to the post-anthesis movement of the flowers. A similar time delayed development of a sclerenchymatous sheath coupled to a pedicel rotation has also been observed in *Convallaria* (Utech and Kawano, 1976b) and in *Streptopus*, *Clintonia*, and *Polygonatum*

(Utech, unpublished manuscripts). The deciduous tepals in *Medeola* are lost by the time the pedicel is erect.

Tepal Vascularization

Although vascularization of the two tepal whorls is identical, the traces to the two whorls do depart in two vertically separated planes. Prior to the divergence of the three lower OTM, all six of the larger pedicel bundles (P) become broadly crescent-shaped and divide radially to form an inner ring of 12 bundles which are distinct and separate from the two sets of tepal medians (Figs. 1C, 4, 5). Following this division, where previously a single P bundle had occurred between an outer (OTM) and an inner (ITM) tepal median, there are now two half P bundles. Tepal laterals (TL) arise from these P bundle halves at the same level as their respective medians (OTM or ITM) depart. Clearly the P bundles are compound bundles.

On both sides of an OTM, there is a P bundle half. Within a given outer tepal, the two basal tepal laterals (TL), which depart with the OTM, originated in a different P bundle halves via radial division (Fig. 5). A similar pattern of division occurs among two different P bundle halves in the formation of the inner tepal laterals (TL). At this latter receptacle height, within a 60° circumference of a cross-section, the following bundles can be found: an unbranched, departing OTM; an outer tepal lateral (TL) arising from a vertical continuing P bundle half; the other P bundle half, which branches to give an inner tepal lateral (TL); a soon-to-depart ITM (Fig. 5).

The manner in which the outer and inner tepals are cut off from the receptacle base, as well as their size and shape, are exactly the same. Neither staminal epitepaly nor lateral syntepaly occurs basally (Figs. 1D, 2C-D). Nectiferous tissue and pubescence are absent from both tepal cycles. At its level of attachment, each tepal receives three traces, that is, its median (either OTM or ITM) and two tepal laterals (TL) (Fig. 5). Neither branching nor fusion of the tepal medians occurs within the laminal tepal surface. The tepal laterals, on the other hand, each undergo two radial divisions after the tepal based is freed from the receptacle. Subsequently, each mature tepal has seven veins, that is, three TL plus median plus three TL.

Stamen Vascularization

Following the radial formation of the 12 half bundles and the subsequent one-sided division and departure of the outer tepal laterals from six of the half bundles, another radial division occurs among these same six P bundle halves. These resulting branches are on the same side of their parental bundles as the previously derived outer tepal laterals. Each of the three separate paired sets of such branches fuse

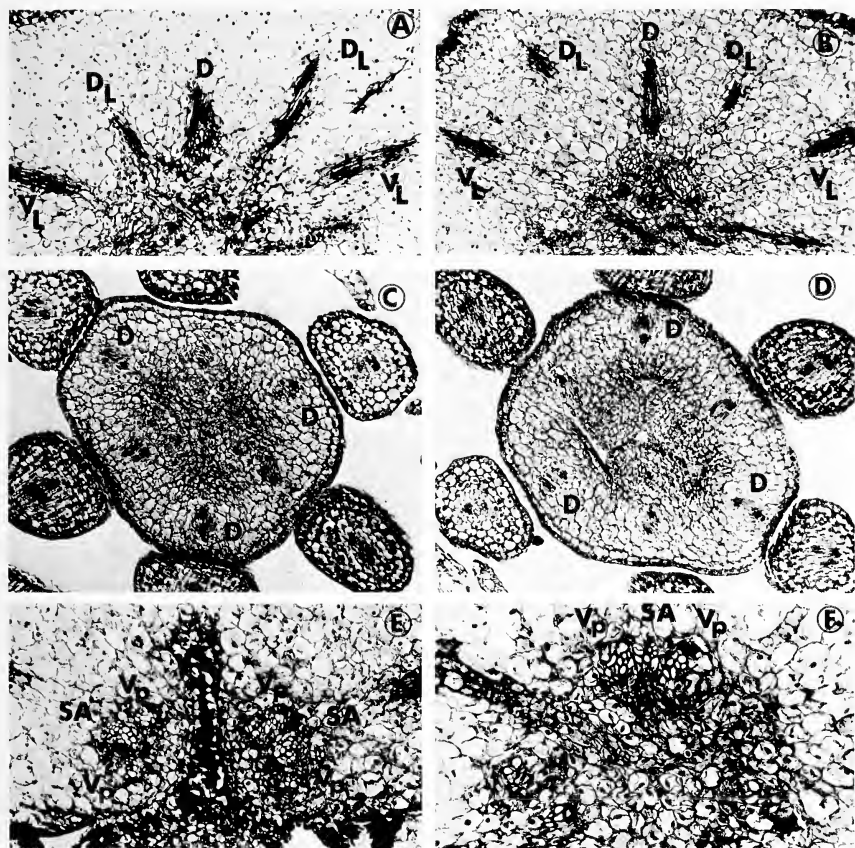


Fig. 2.—Vascularization of *Medeola virginiana*. A. Gynoecial base cross-section showing the departure of a fusion dorsal (D) with two associated dorsal laterals (D_L), as well as two fusion ventral laterals (V_L). Ventral plexus bundles remain (125 \times). B. Similar to A, but a higher section (125 \times). C. Central opening of the locules. No dorsal grooves evident. Both ventral laterals and ventral plexuses evident along the septal radii. (35 \times). D. Closing of the ventral laterals still present, whereas the inner ventral placentals are ending (35 \times). E. Enlarged cross-sectional view of a mature flower showing two septa with their two ventral placentals (V_p) and a central septal axial (SA) (150 \times). F. Lower cross-section than in E showing the two ventral placentals (V_p) and a median septal axial (SA) (150 \times).

along the three OTM radii and form the three outer stamen traces (OS). Each OS is separated by 120° and their formation closes the gap along the OTM radii (Fig. 5).

The six remaining and continuing P bundle halves (three pairs) which had branches to form the OTM and the OS traces, then fuse in pairs to

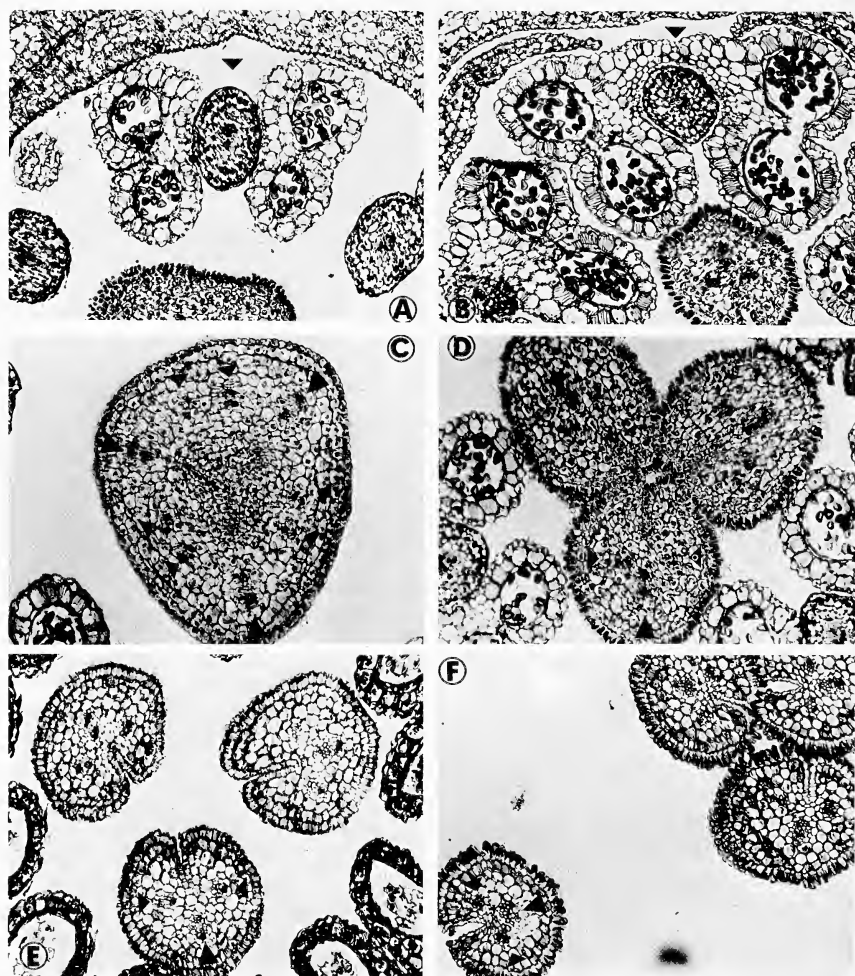


Fig. 3.—Vascularization of *Medeola virginiana*. A. Stamen cross-section, the triangle indicates the shorter, inner filament with its associated anther sacs, in the lower right is a longer, outer filament (35 \times). B. Stamen cross-section, higher section than in A, the triangle indicates an outer stamen with its filament still unattached to the anther, whereas the filament and anther of an inner stamen in the lower left are attached. Extrorse condition and the banded epithelial thickenings are evident (35 \times). C. Cross-section through the common hollow style, the ventral laterals have divided into pairs of bundles (paired triangles), dorsals indicated (large triangles) (35 \times). D. Cross-section showing the formation of the 3 styler arms, each arm has 3 bundles, the continuing dorsal and two branch bundles from different ventral laterals (small triangles) (35 \times). E. Cross-section above D showing the free styler arms, the styler furrows are directed away from the surrounding anther zone. (35 \times). F. Styler cross-section above the stamens showing in the lower left one of recurved styler arms with its outward directed styler furrow (35 \times).

form the three carpel dorsals (D). Both the outer stamen traces and the dorsals (D) are fusion products involving the same six P bundle halves. Again, this repeated division of the P bundles attests to their compound nature.

The origin of the inner stamen traces (IS) is similar to that of the outer stamen (OS) traces (Fig. 5). The previously uninvolved and remaining six bundle halves form lateral branches via radial division. These new branches are on the same side of their parent bundles as the inner tepal laterals. These new lateral branches then fuse along the ITM radii and form the inner stamen traces (IS). Their formation closes the gap along the inner tepal median radii. There are three IS traces so formed, each 60° from an adjacent OS trace.

The remaining six parent bundle halves which branched to give rise to the inner stamen traces fuse subsequently along the common ITM-IS radii (really the septum) to form three independent plexuses, which constitute the lateral and ventral supply system (Fig. 1D).

The six stamens are freed directly in two cycles from the hypogynous gynoecial base (Figs. 1D, 2C–D). Neither raphides, epidermal pubescence, epitepaly nor lateral stamen fusion occurs within the two stamen cycles. The inner three filaments are slightly longer (ca. 1 mm) than the outer three filaments (Fig. 3A–B). All six dorsifixed anthers have identical lengths within both cycles. The adaxial point of filament attachment is the same within both cycles, but due to the differential filament length, the effective height of the presented anther zone is greater than the length of an individual anther (Fig. 3A–B). The morphological variation in cycle filament length increases the pollen dispersal zone, because the anthers dehisce via lateral, vertical slits (extrorse condition). The epitepical cell walls lining the stamen sacs have banded thickenings (Fig. 3B). Each stamen receives a single fusion trace. The base of the gynoecium contains essentially six fusion product bundles each separated by 60°—the three dorsals (D) and the three ventral plexuses (Figs. 1D, 2C–D, 4, 5).

Gynoecial Vascularization

The oval-oblong, tricarpellate gynoecium of *M. virginiana* lacks notches or grooves over the dorsals. Septal glands or indentations are also lacking. When present in other liliaceous species such glands frequently function as nectaries. Because septal glands are lacking, the three carpels of the ovary are completely fused along the outer septal margins. The inner septal margins are, however, free on their wing tips from each other throughout the ovary length (Fig. 2C–D). The tricarpellate ovary, therefore, must be considered unilocular. The resulting common hollow ovary cavity is continuous with the common hollow stylar canal. The gynoecium terminates in a very short common style,

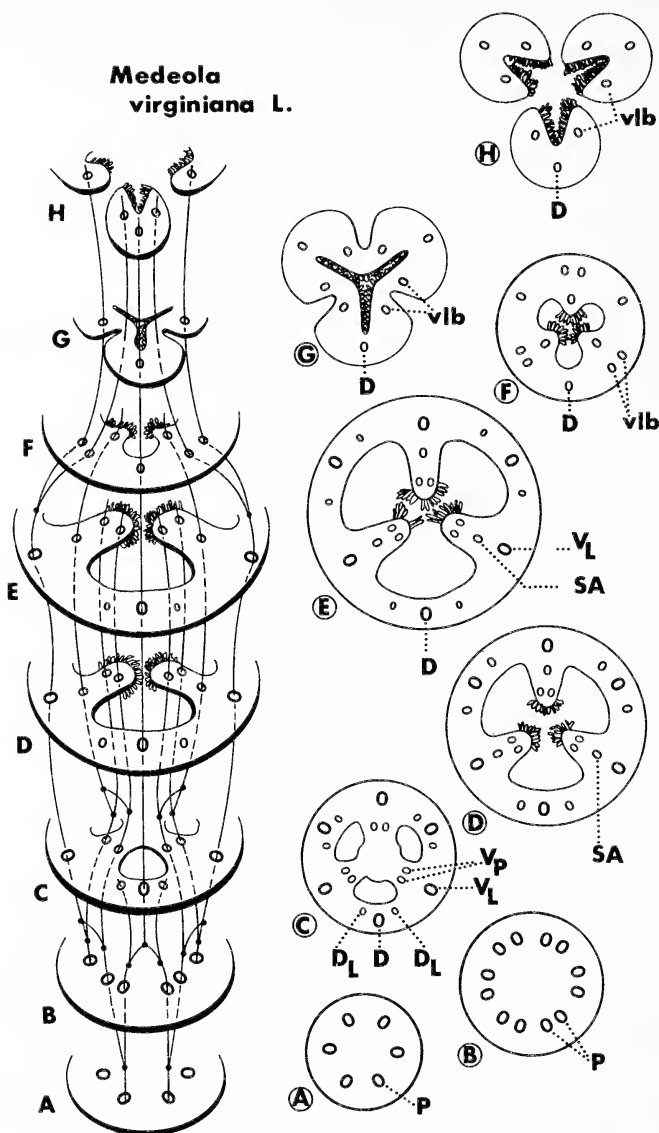


Fig. 4.—Serial cross-sections of *Medeola virginiana* and their associated projections that have had the various bundles connected. The series runs from the mid-pedicle to the region of the three free stylar arms. The formation of the tepal and stamen traces are not indicated.

which is divided into three long style-stigmata branches (Fig. 3C-F). The common style along with the three long stigmata branches is deciduous and leaves a terminal, circular ovary scar.

Dorsal Supply

Basically, the gynoecium has six fused sets of P bundle halves. Fig. 4 does not show the derivation and departure of the tepal and stamen vasculature, only the gynoecial vascularization is presented. The three dorsals (D) are fusion products formed from three paired sets of receptacle P half bundles and lie along the OTM-OS radii.

There is a movement of the newly formed dorsals (D) outward so as to pass under the unopened locules (Fig. 2A-B). As the three locules do open, two minor lateral branches depart on each side of the three fused dorsals (D). These side branches, designated dorsal laterals (D_L) ascend upwards, parallel with their dorsal in a subtending, outer locule position (Figs. 2A-B, 4, 5). The D_L do not fuse terminally with their parent dorsals or branch further, but simply terminate in the upper gynoecial areas. The dorsals (D), on the other hand, continue up into the common style unbranched, and terminate in the recurved stigma tips (Figs. 3D-F, 4, 5).

Ventral and Lateral Supply

The ventral supply which involves both laterals (V_L) and septal axial (SA) in addition to the placental supply (V_P) is far more complex than that reported for the dorsal (D) supply. The three remaining sets of paired bundle halves at the base of the gynoecium constitute the source for the total lateral and ventral supply (Figs. 1D, 2C-D).

At a level above that at which the dorsals (D) are formed, two adjacent bundle halves, which had branches to form the ITM and IS traces, branch again. These two branches then fuse and form a bundle which lies along the septum radius, which is also the ITM and IS traces. This new fusion bundle is the ventral lateral (V_L). There are three of them each 120° apart (Fig. 2A-B, 4, 5). Their formation is analogous to that of the dorsals (Figs. 4, 5). Their position of formation, like that of the dorsals, means that the V_L exhibit a net outward movement.

As two dorsal laterals (D_L) are associated with a given dorsal (D), similarly two traces remain and continue upwards in the septal areas following the formation of the outer ventral laterals (V_L) (Figs. 4, 5). With locule opening these continuing traces (3 paired sets) move inwards along the septal radii and establish the placentals (V_P) and septal axials (SA) within each septum (Figs. 2E-F, 4, 5).

The unilocular condition arises through the freeing of the fused inner septal margins near the gynoecial base (Fig. 2C). At this level, the three pair of continuing ventral bundles have moved to the inner septal wing

margins. Here another fusion product, the septal axial (SA), is formed via branches from each of two placental bundles (V_P) in each septum that fuse (Fig. 2E-F). Three of these bundles (SA_1 - SA_3) are so formed (Figs. 4, 5). They lie along the same radius as the ventral laterals (V_L). One peculiar characteristic of the septal axials (SA) is the reversal of their xylem and phloem in relations to all of the other bundles. The septal axials (SA) and the two associated ascending placental bundles (V_P) per inner septal wing margin show no signs of cross-connection throughout their vertical ascent and all three terminate in the upper gynoecial region. (Figs. 2D, 3C, 4, 5).

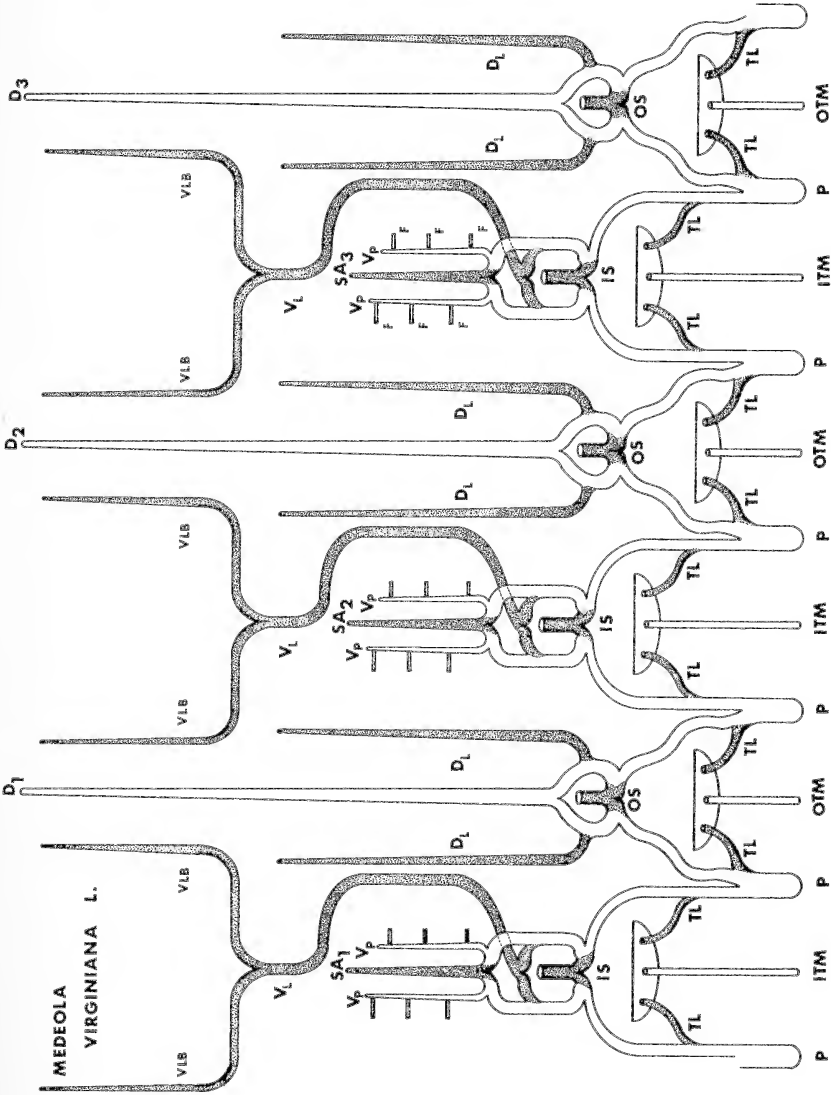
It should be noted that the dorsal laterals (D_L), the septal axials (SA), and the ventral system (placentals— V_P and funicular traces—F) are not observed in sections of buds or early flowering material. They are definite, however, in the more mature flowers and early fruits. The summary diagrams (Figs. 4-5) present these bundles, but it must be remembered that they do not occur in the younger material.

Horizontal funicular (F) branches arise in alternate ranks from the parallel placental bundles (V_P) within each of the three septa (Fig. 5). A maximum number of 18 ovules was observed, that is, six funicular branches (F) per septum or three funicular branches per placental bundle. Because the placental (V_P) and their associated funicular branches (F) are ranked alternately on different sides of the fused margin of two different carpels and the supplied ovules have a vascular supply from two and not one carpel, (Figs. 4, 5), the placentation is parietal (see also Berg, 1962a). Initially, the ovules have a pleurotropic orientation, but following fertilization their orientation changes to a more hypotropous condition. There is a further differential shifting of the developing seeds especially in the upper tier of the mature fruit, such that the resultant seed packing could best be described as heterotropous (terminology after Björnstad, 1970).

The greenish flowering gynoecium is relatively small (diameter, 3-4 mm) compared to that of the globose, purplish-blue berry fruit (diameter, 9-15 mm). The fruit is indehiscent (there were no notches or grooves in the flower to indicate weakness zones) and pulpy. The

→

Fig. 5.—Vascularization summary diagram for *Medeola virginiana* showing the following text introduced and discussed bundles and traces: TL = tepal laterals; OTM = outer tepal median (three); ITM = inner tepal median (three); P = large pedicel bundle (six); OS = outer stamen (three; fusion product); IS = inner stamen (three; fusion product); D = dorsal (three; fusion product); D_L = dorsal lateral (three pairs); V_L = ventral lateral (three; fusion product); vlb = ventral lateral branch (three pairs); V_P = ventral placentals (three pairs); SA = septal axial (three; fusion product).



increase in size is chiefly due to the increase in the seed volume and a parenchymatic increase in the number of cells in the pericarp.

Style-stigma and the Stigmatoid Tissue System

In the upper gynoeceium, the following vertically ascending bundles end: the dorsal laterals (D_L); the septal axials (SA_1 - SA_3); the six placental bundles (V_P) (Figs. 2D, 4, 5). The three dorsals (D) and the three ventral laterals (V_L), on the other hand, continue. There is a common hollow style which extends for about 1 mm above the top of the ovary. This style is circular in cross-section at its base, but quickly becomes broadly trilobed as the style branches are freed (Fig. 3C-F).

Below the common stylar region, a most unusual division occurs within the ventral laterals (V_L). Each V_L divides in half and the two resulting branches (vlb) reassociate laterally with the two dorsals adjacent to them (Figs. 3C-F, 4, 5). With the common style divided into three free stylar arms, three bundles are found in each arm—the continuing dorsal (D) and the two ventral lateral branches (vlb) (Figs. 3C-F, 4, 5). These three bundles continue to the extreme recurved tips of the stylar arms (Fig. 3F).

Each style is deeply grooved or notched with a papillae-lined furrow that runs the entire length of the elongated style-stigmata (Fig. 2C-F). Because the flower with its short filaments and small anthers is inverted at anthesis, the three stylar arms which are recurved terminally over the anther tips function to exclude pollen from the same flower. The receptive pollen grooves are directed away from the same flower's pollen dispersing zone. This stylar adaptation would certainly reduce inbreeding for that flower while at the same time promote outbreeding. The papillae of the stylar furrows are continuous into the common stylar region and also cover the inner edges of the septal wings. Such papillae cell distribution constitutes a supportive stigmatoid tissue system, which is directly related to the path of pollen tube growth.

DISCUSSION AND CONCLUDING REMARKS

In his classical revision of the North American Liliaceae, Watson (1879) placed *Medeola* in his tribe Trillieae subtribe Medeoleae with *Trillium*. *Scoliopus* was placed in the other subtribe (Scoliopeae). *Paris* is strictly an Old World genus. The taxonomic association of *Medeola* and *Trillium* can be dated to this monograph.

Baker (1876) associated *Medeola* in his tribe Streptopeae with *Clin-tonia*, *Prosartes* (= *Disporum* section *Prosartes*), *Disporum* (=section *Eudisporum*), *Streptopus*, and *Kruhsea* (= *Streptopus*). Today all of these genera except *Medeola* are placed in the tribe Polygonatae. In the Englerian system (Engler, 1888; Krause, 1930), *Medeola* is placed in the small, but advanced liliaceous tribe Parideae along with *Paris*,

Trillium, and *Scoliopus*. In recent years, this tribe has been alternatively segregated from the Liliaceae as the family Trilliaceae (Hutchinson, 1934) with *Trillium* rather than *Paris* serving as the type genus. Because *Medeola*, *Trillium*, and *Paris* are all Linnaean genera (1753), their order of printed appearance should be important—*Medeola* (n. 455; p. 339), *Trillium* (n. 456; p. 339–340), and *Paris* (n. 500, p. 367). Clearly *Medeola* is the oldest and indeed should be the valid generic basionym for tribal and/or familial rank, if the group is maintained.

Bentham and Hooker (1883) put *Medeola* in their tribe Medeoleae following the printed Linnaean order noted above and the subtribal ranking of Watson (1879). Their tribe included *Medeola*, *Paris*, *Trillium*, *Scoliopus*, and *Clintonia*. The latter has long since been removed from this association (review Utech, 1973), and has been placed in the tribe Polygonatae (Engler, 1888; Krause, 1930; Hutchinson, 1934).

Based on a partial analysis of the vascular floral anatomy of *Medeola* and several *Trillium* species, but not on that of *Paris* and *Scoliopus*, Anderson (1940) suggested a transfer of *Medeola* from the Englerian Parideae to a position near the tribe Tulipeae of the subfamily Lilioideae. Using embryology and gross floral morphology, Berg (1962a, 1962b) also proposed the removal of *Medeola* from its tribal (or familial) grouping with *Paris*, *Trillium*, and *Scoliopus*, and further suggested placing *Medeola* in its own tribe (Medeolideae) in the same subfamily (Lilioideae) as Anderson (1940).

Medeola virginiana with a somatic chromosome number of $2n = 14$ ($n = 7$) (Stewart and Bamford, 1942; Woodard, 1948) is characteristic of the $x = 7$ base number so prevalent in the Lilioideae (Darlington and Wylie, 1955; Federov, 1969; Moore, 1973), whereas *Paris* and *Trillium* share a common $x = 5$.

Furthermore, Berg's work (1959, 1962b) on the embryology and gross floral morphology of *Scoliopus* indicates a high dissimilarity between *Scoliopus* and *Medeola*, as well as a dissimilarity between them and the two other members of the Parideae, *Paris* and *Trillium*. The latter two, on the other hand, do show a high degree of similarity. *Medeola* and *Scoliopus*, though dissimilar, both have affinities with the subfamily Lilioideae.

Berg's conclusion which relates the affinities of *Medeola* and *Scoliopus* to the Lilioideae was also supported and discussed by Björnstad (1970) in his comparative embryological study of the closely related Englerian tribe Polygonatae and his subsequent comparison to Berg's work on the Parideae (1959, 1962a, 1962b).

The taxonomically important berry fruit so crucial in delineating certain Englerian subfamilies and tribes may well represent a unit of convergent evolution. Though the liliaceous berries are superficially similar and useful (visually) taxonomically, they may not at all reflect a

natural relationship. The bird dispersal of these red, blue, and black berries so common in the forest environments would be a selective pressure for this type of convergent evolution.

It is hoped that the detailed examination of the total vascular floral anatomy which underlies the liliaceous berry can be used in establishing lines of natural relationships. It is from this point of view, that the floral anatomy of *Medeola* is here presented. Similar investigations are currently in progress on *Scoliopus*, *Trillium* and *Paris*, as well as other members of the berry-fruited tribe Polygonatae.

SUMMARY

The total floral vascularization of *Medeola virginiana* results from two different sets of six pedicel bundles. A sclerenchymatous sheath differentiates the flowering from the fruiting pedicel. The lower pedicel contains a double ring of six inner and six outer bundles. The six outer bundles establish the three outer and three inner tepal medians directly in two whorls without fusion or branching. The six inner bundles, on the other hand, are clearly compound and undergo several radial divisions each. These divisions are subsequently followed by various whorl-separated levels of fusion. The lower whorl division results in the formation of six (three sets of two) outer tepal laterals. No fusion is associated with the formation of the tepal laterals, but they do branch further in laminal tepal surface. Each tepal has seven parallel veins, that is, three TL plus median plus three TL.

Further division and fusion of the continuing inner pedicel bundles result in the formation of the six stamen traces (both whorls), the three dorsals, the six dorsal laterals, the three ventral laterals, the six ventral placentals, and the three sepal axials. The stamen, dorsal, ventral lateral, and septal axial traces are all fusion products.

The tricarpellate gynoecium is unilocular, because the septal wing tips are free at the gynoecial base. This species lacks raphides, septal glands, and dorsal notches. Three bundles (that is, continuing dorsal plus two branches from different ventral laterals) occur in each of the three recurved stylar arms. Papilloid cells line the three inner notched stylar arms and are continuous downward through the common hollow stylar canal to the base of the gynoecium.

In flower, the pedicels are directed downwards, whereas in fruit, they are erect. The development in the fruiting pedicel of a sclerenchymatous sheath around the vascular bundles may be related directly to upward shift of the pedicel. The pendulent flower, on the other hand, has a style-stigma system which excludes its own pollen due to the location of the outward directly stylar furrows and the long, recurved stylar tips. The extrorse anthers also promote outbreeding. The flowering gynoecium is relatively small compared to the size of the resulting

fruit. A maximum number of 18 ovules (six/carpel) is not uncommon. The ovule arrangement is variable.

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ARTICLE 3

SOUTHERN FORMS OF *CHIRINDIA* (AMPHISBAENIA, REPTILIA)

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ABSTRACT

The southern specimens of the African amphisbaenian genus *Chirindia* may all be assigned to the species *C. swynnertoni* (including *C. bushbyi*) from Rhodesia and Mozambique, and *C. langi* from Transvaal, South Africa. *C. swynnertoni* is also redefined versus the similar form *C. orientalis* from southern Tanzania. The snakes of the genus *Cryptolytus* appear to be specialized predators on these small amphisbaenians.

INTRODUCTION

The four Tanzanian species of *Chirindia* have been described in an earlier paper (Gans and Rhodes, 1967). The present review deals with the southern forms of *Chirindia*, which inhabit central Mozambique, adjacent Rhodesia and the northeastern Transvaal, and are separated from the Tanzanian populations by a space of 800 km. The three nominal southern species, *C. langi*, *C. swynnertoni*, and *C. bushbyi*, were each described from one or two specimens. Few additional specimens have been recorded (Broadley, 1966; Pienaar, 1966). Systematic collecting has now increased the total number of southern specimens to 155, enabling us to analyze their variation.

The southern *Chirindia* localities fall into two areas (Fig. 1)—

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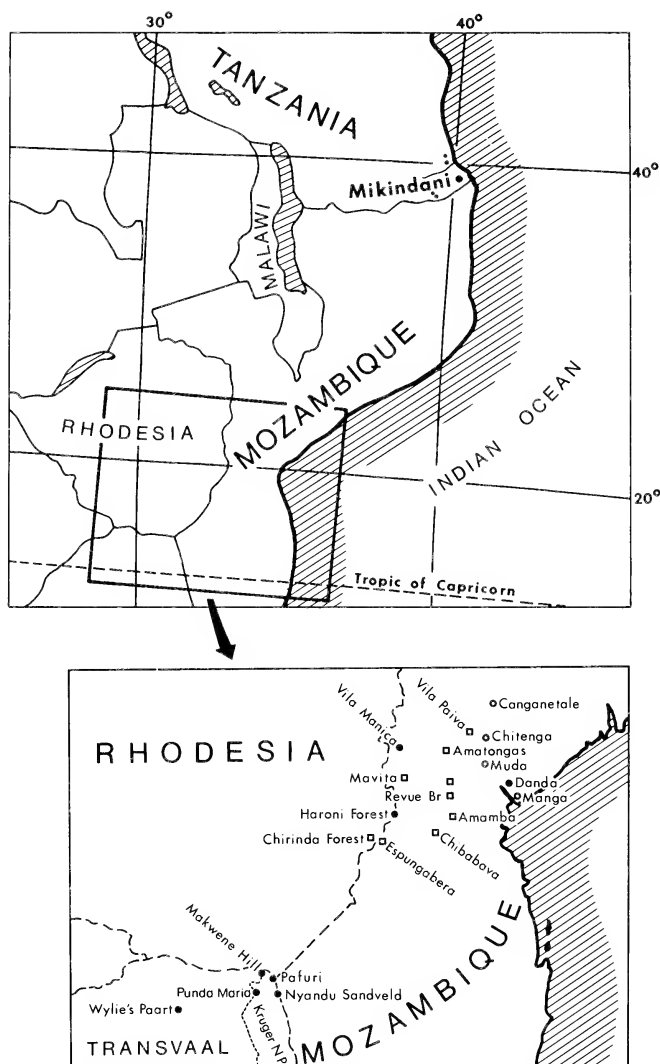


Fig. 1.—Sketch maps showing localities mentioned in the text. All those within the Kruger National Park lie within the area delineated by the four localities plotted therein. Those on Urema/Pungwe floodplain are shown by open circles, “Miombo” localities by squares.

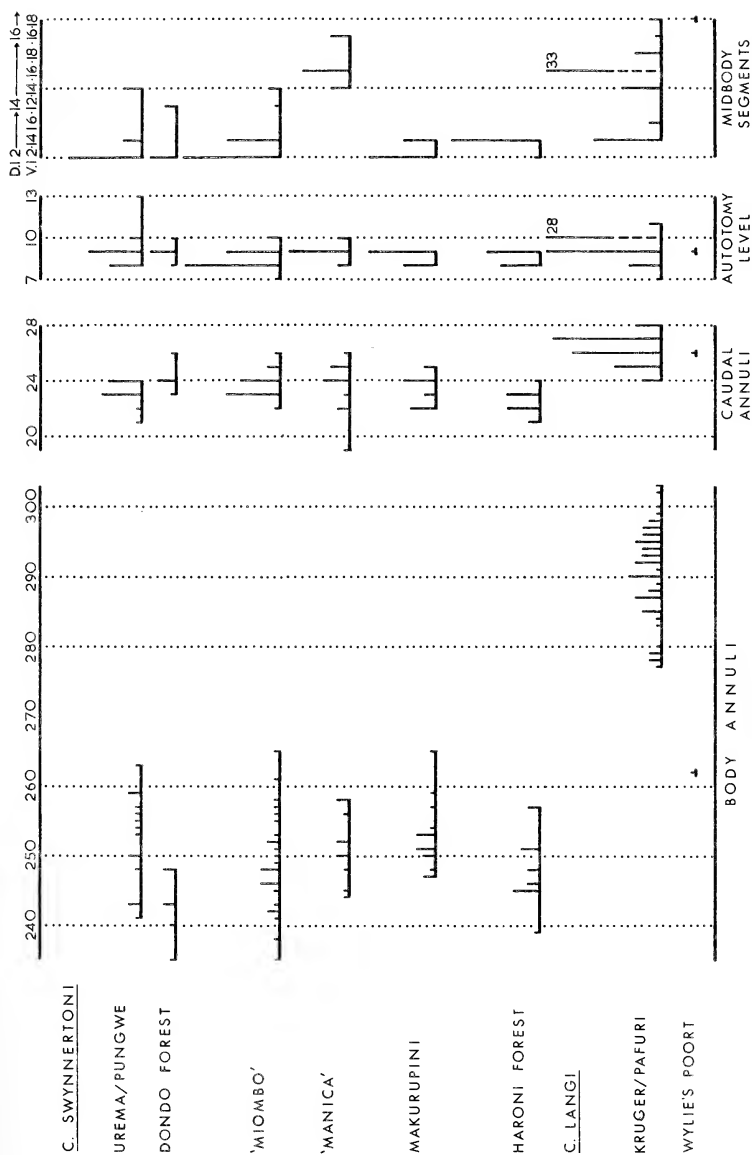


Fig. 2.—*Chirindia*. Diagram showing frequency distribution for number of annuli and midbody segments for the several samples.

material from the northeastern Transvaal agrees with the type of *C. langi* in having a discrete second supralabial, which incorporates the ocular, whereas material from central Mozambique and adjacent Rhodesia agrees with the type of *C. swynnertoni* in having the ocular and second supralabial fused with the enormous prefrontal/nasal/first supranasal. *Chirindia orientalis* of coastal Tanzania is superficially similar to *C. swynnertoni* and could prove conspecific with it, assuming that the lack of records from northern Mozambique is due to the scanty herpetological collections from this intermediate region.

ACKNOWLEDGMENTS

We are grateful to the following curators of institutions (identified throughout by the abbreviations given in parentheses) for permission to borrow or examine material in their care: Miss Alice G. C. Grandison of the British Museum of Natural History (BM); Carl Gans collection, Ann Arbor (CG); Dr. U. de V. Pienaar of the Kruger National Park (NKW); Dr. J. A. Pringle of the Natal Museum (NMP); Mr. Wulf Haacke of the Transvaal Museum (TM); Umtali Museum (UM); and Dr. G. Peters of the zoologisches Museum der Humboldt Universität, Berlin (ZMU). Some material has been deposited in the Carnegie Museum of Natural History (CM). Supported by NSF grant DEB-76-18289.

COMMENTS ON THE LOCALITIES

The ninety specimens of *C. swynnertoni*, which came from 17 localities, were divided for analysis into six groups based on habitat. The first group (Urema/Pungwe) includes 17 specimens from Canganetole (8), Chitengo (1), Muda-Lamego (2), and Manga (6)—all localities on the extensive floodplain that marks the old lower course of the Zambezi, terminating at the Pungwe Estuary. These alluvial flats are covered with extensive grasslands, but the Chitengo specimen was taken in the middle of a thicket, and the Manga series were plowed up in a cultivated area. The Muda-Lamego specimens were trapped in an oil-pipeline trench.

Most of the evergreen forest in central Mozambique has been destroyed by charcoal burners or by others clearing land for cultivation. Dondo Forest survived because it is a chiefs' burial ground. A small series of *Chirindia* ("Dondo") was collected by Broadley from rotting logs in this forest.

The third group ("Miombo") consists of 25 specimens from 25 km south of Vila Paiva de Andrada (1), Amatongas (1), 25 km north of Revue Bridge (1), Revue Bridge (1), Amamba (15), near Chibabava (2), Mavita (1), Espungabera (2), and Chirinda Forest (1). Although these are all from basically miombo woodland habitats, the specimens from near Chibabava were under slabs of limestone, the Mavita specimen was under a flake lying on a granite outcrop, and the Espungabera specimens were under boulders on a hillside above the Buze River. The type came from the crop of a kingfisher (*Halcyon albiventris*) shot on the

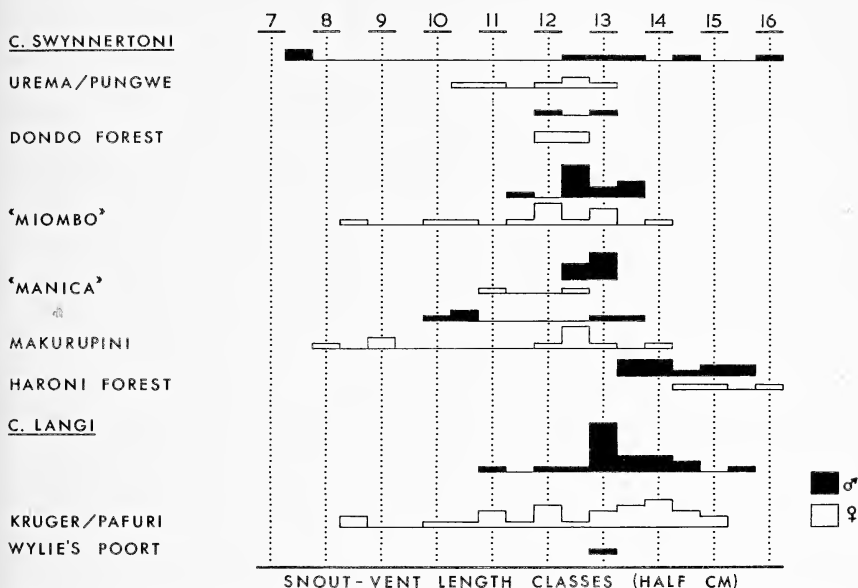


Fig. 3.—*Chirindia*. Histogram showing number of specimens of the various samples in the different snout-vent length classes. Each class covers 5 mm, that is, class 7 = 70 to 74 mm inclusive. The smallest vertical unit indicates one specimen. Specimens with pores are classed as males and specimens lacking pores as females.

edge of the Chirinda Forest, but the bird is a savanna species and probably picked up the *Chirindia* in nearby miombo woodland. Intensive collecting in Chirinda Forest itself has never yielded any amphisbaenians, and *Zygaspis quadrifrons* is the only species that has been taken in the vicinity.

A series of 13 *Chirindia* collected 25 km southeast of Vila de Manica ("Manica") differs from all other populations of *C. swynnertoni* in their high counts of midbody segments (Fig. 2). They were taken under granite boulders in miombo woodland on sandy soil at the foot of a granite *inselberg*.

A Rhodesian Schools' Exploration Society Expedition to the southern end of the Chimanimani National Park in 1969 obtained a fine collection of *Chirindia* from the Makurupini Valley. Fourteen specimens were collected in dense evergreen forest (Haroni Forest) on the west bank of the Makurupini River, and 15 specimens were taken in *Uapaca* (Mahobohobo) woodland along the Mozambique border on the east bank. These series have been kept separate for comparative purposes.

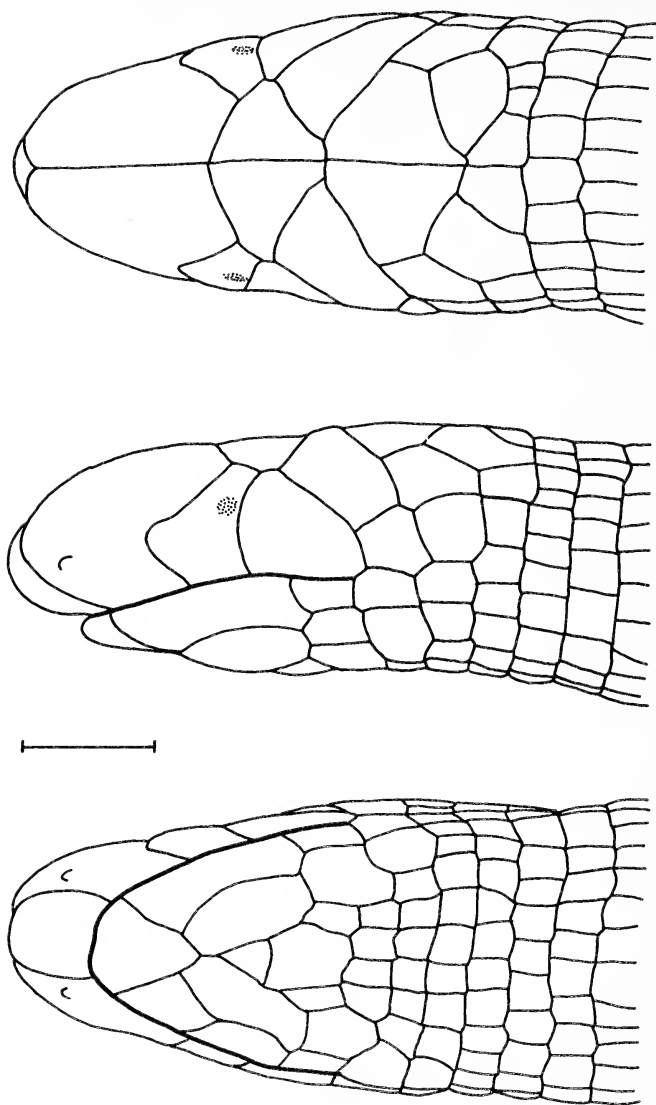


Fig. 4.—*Chirindia langi*. Dorsal (top), lateral (middle), and ventral (bottom) views of the head of TM 26,317 from Hape Pan, Pafuri, Transvaal, to show the sulci and segment proportions and pigmentation. The line equals one mm to scale.

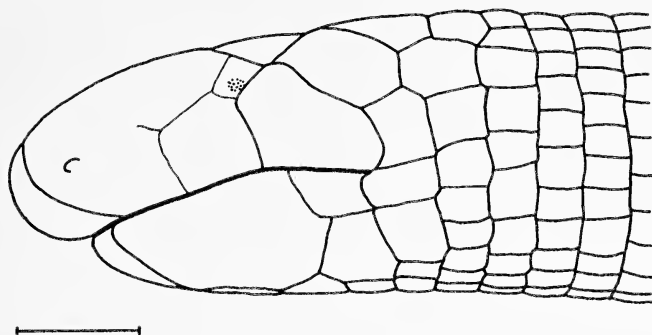


Fig. 5.—*Chirindia langi*. Lateral view of TM 28,867 from Pafuri to show ocular and accessory supralabial. The sutures separating all these scales are very much less deeply incised than the remaining ones.

The bulk of the available *Chirindia langi* material was turned up by bulldozers cutting firebreaks in the northern areas of the Kruger National Park. These amphisbaenians were usually found in areas of “msimbiti” (*Androstachys johnsonii*) thicket (Pienaar, 1966).

The Wylie’s Poort specimen was found under a stone near the main road to Messina, just north of the Soutpansberg, by Dr. W. R. Branch.

COMPARISON OF SOUTHERN FORMS OF *CHIRINDIA* WITH THOSE OF TANZANIA

The most northerly (*C. mpwapwaensis*) and southerly (*C. langi*) forms of *Chirindia* appear to be the most primitive. These peripheral taxa are the only members of the genus to retain a discrete second supralabial (plus a discrete ocular in the two known *C. mpwapwaensis* and occasionally in *C. langi*), and they have high counts of segments in a midbody annulus. *Chirindia langi* has the highest counts of body annuli (277–303) found in the genus, but the unique specimen from Wylie’s Poort has only 262 body annuli, fewer than *C. mpwapwaensis* (266–272).

Chirindia swynnertoni agrees with the two previous species in having a rounded snout and the parietal separated from the post-supralabials. It is also similar in size. It has fewer segments in a midbody annulus and fewer midbody annuli (235–265). *Chirindia orientalis* (Sternfeld) of Mikindani, southeast Tanzania, is very similar to *C. swynnertoni* in number of caudal annuli (22–23), pore number (5–6/0), rounding of head, and scale proportions. However, it does differ by having a few more body annuli (range = 257–271; mean = 262.4), a relatively shorter tail (following the trend shown in Gans and Rhodes, 1967: Fig.

6), a tendency to fewer (12–14 dorsal/10–12 ventral) segments to a midbody annulus, and in always retaining a postmental segment. It has now become possible to examine the entire type-series of *C. orientalis* in the Berlin Museum (ZMU 22067, 22407A–C, 28408A–B, 28409). This turns out to comprise nine rather than the seven specimens initially mentioned by Sternfeld (1911). The foregoing statements are based upon this material. In morphology *Chirindia swynnertoni* and *Chirindia orientalis* are intermediate between the relatively primitive forms *C. mpwapwaensis* and *C. langi* and the dwarfed species *C. ewerbecki* and *C. rondoensis* of southeastern Tanzania. In the latter species the postoculars are always in broad contact, and the snout is rather pointed.

VARIATION OF CHARACTERS

Body Annuli.—The highest counts (277–303) are from the northern Kruger National Park and adjacent Pafuri Game Reserve, the unique Wylie's Poort specimen having a considerably lower count (262). The grouped "Miombo" sample has a range (235–265) similar to that of the entire remaining populations of *C. swynnertoni*. The two samples from evergreen forests have lower average counts ("Dondo," range = 235–248, mean = 242.8; "Haroni," range = 239–257, mean = 248.1), than those from neighboring savanna habitats ("Urema/Pungwe," range = 241–263, mean = 250.3; "Makurupini," range = 247–265, mean = 252.6). Among the "Miombo" sample, above-average counts (257, 265) were recorded for the two specimens from the limestone ridge east of Chibava.

Caudal Annuli.—Counts of caudal annuli for *C. langi* (24–28) average higher than those for *C. swynnertoni* (19–26). The percentage of autotomized tail is 18.5 for *C. langi* and 16.5 for *C. swynnertoni*.

Autotomy Level.—The usual autotomy annulus is the tenth in *C. langi* and the ninth in *C. swynnertoni* (Fig. 2).

Number of Segments in a Midbody Annulus.—The Tanzanian populations of *Chirindia* show little variation in the number of dorsal and ventral segments in a midbody annulus (Gans and Rhodes, 1967), but within and among the southern populations (Fig. 2) there is considerable variation. In most samples of *C. swynnertoni* the midbody segments are 12/12, 12/14, or 14/14, but in the "Manica" population the counts are 14/14, 14/16, or 16/16, as in the "Kruger/Pafuri" populations of *C. langi*. The highest count is 16/18 for the unique Wylie's Poort specimen.

Head Shape.—The southern species *C. langi* and *C. swynnertoni* have rounded snouts similar to those of *C. mpwapwaensis* and *C. orientalis*. In profile the snout may be swollen with a slight depression in the frontal region.

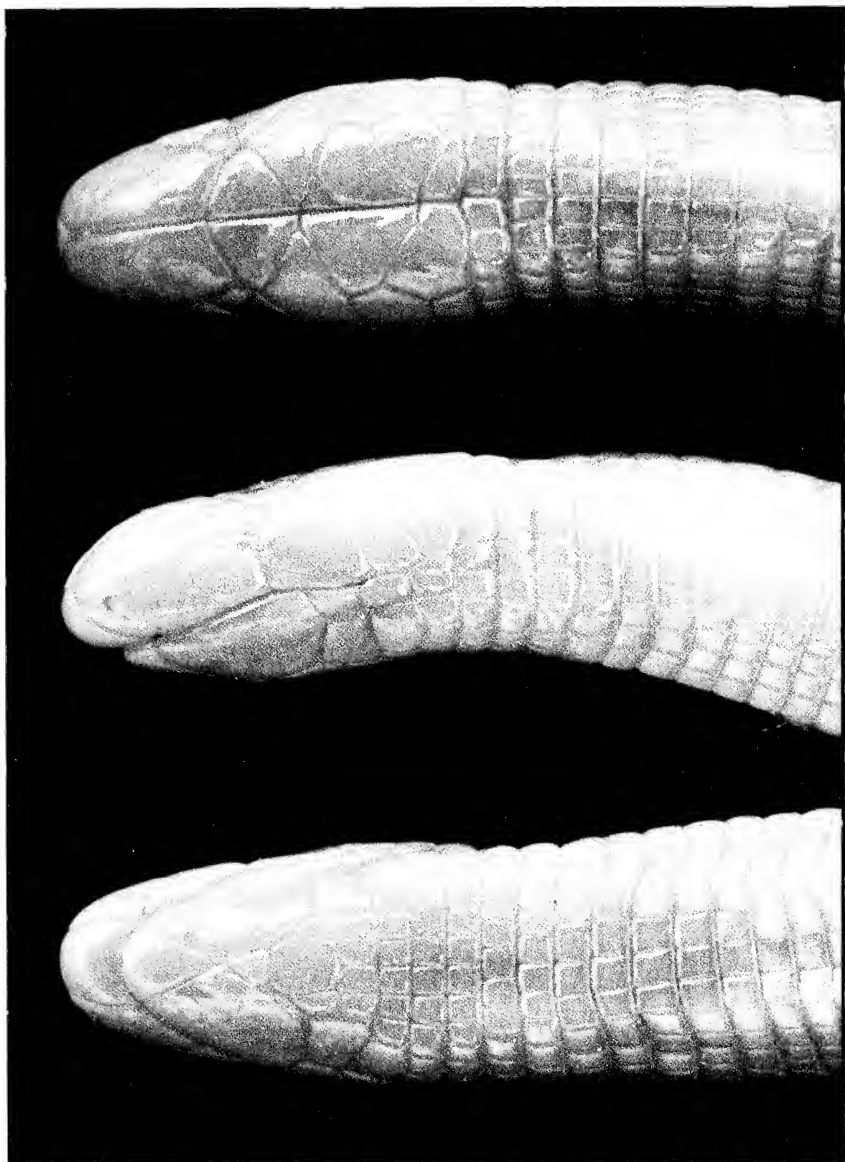


Fig. 6.—*Chirindia langi*. Dorsal, lateral, and ventral views of the head of TM 26,317 to show sculpturing and curvature.

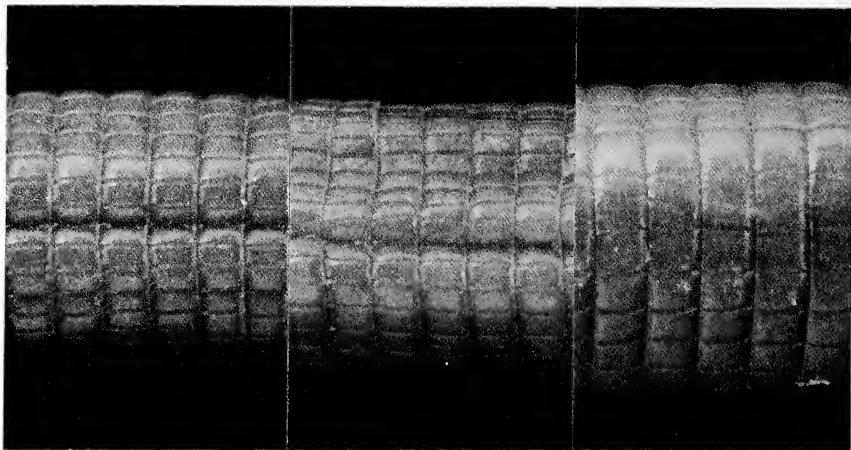


Fig. 7.—*Chirindia langi*. Dorsal (left), lateral (middle), and ventral (right) views at mid-body of TM 26,317.

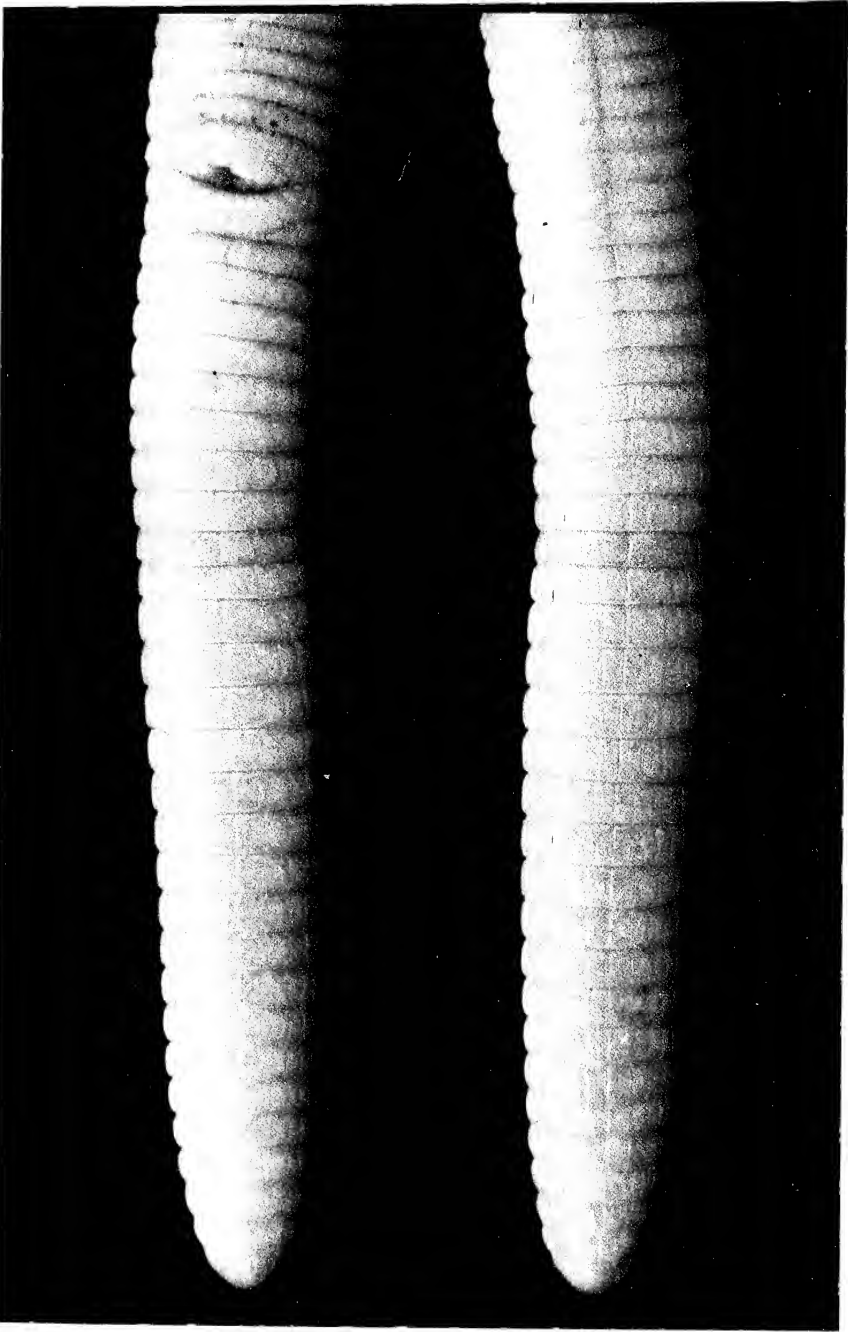
Pattern of Dorsal Head Scalation.—All specimens retain a discrete rostral, although the nasal, first supranasal, and prefrontal on each side are fused to form a pair of very large shields. In several Kruger National Park specimens a short blind suture extends forward from the ocular/second supralabial shield, and on the right side of NKW 309B a long suture extends from the ocular to the rostral, passing above the nostril.

Chirindia langi retains a discrete second supralabial that usually incorporates the ocular. In TM 26317 there is a discrete ocular on the right side and discrete supraocular and ocular on the left side. One specimen (NKW 309B) has the supralabial split into three segments (an upper, a lower anterior, and lower posterior), whereas TM 28867 and NKW 307E have the second supralabial partially fused with the prefrontal. The second supralabial is always completely fused with the prefrontal in *C. swynnertoni*.

The frontals are a pair of small subtriangular shields in broad contact on the mid-dorsal line, and in point or extended lateral contact with the second supralabials. The frontals may be in contact with the parietals posteriorly, or separated by the postoculars making median contact. The parietals are separated from the post-supralabials by one or two

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Fig. 8.—*Chirindia langi*. Ventral and dorsal views of tail of TM 28,867 to show segment proportion and pigmentation.



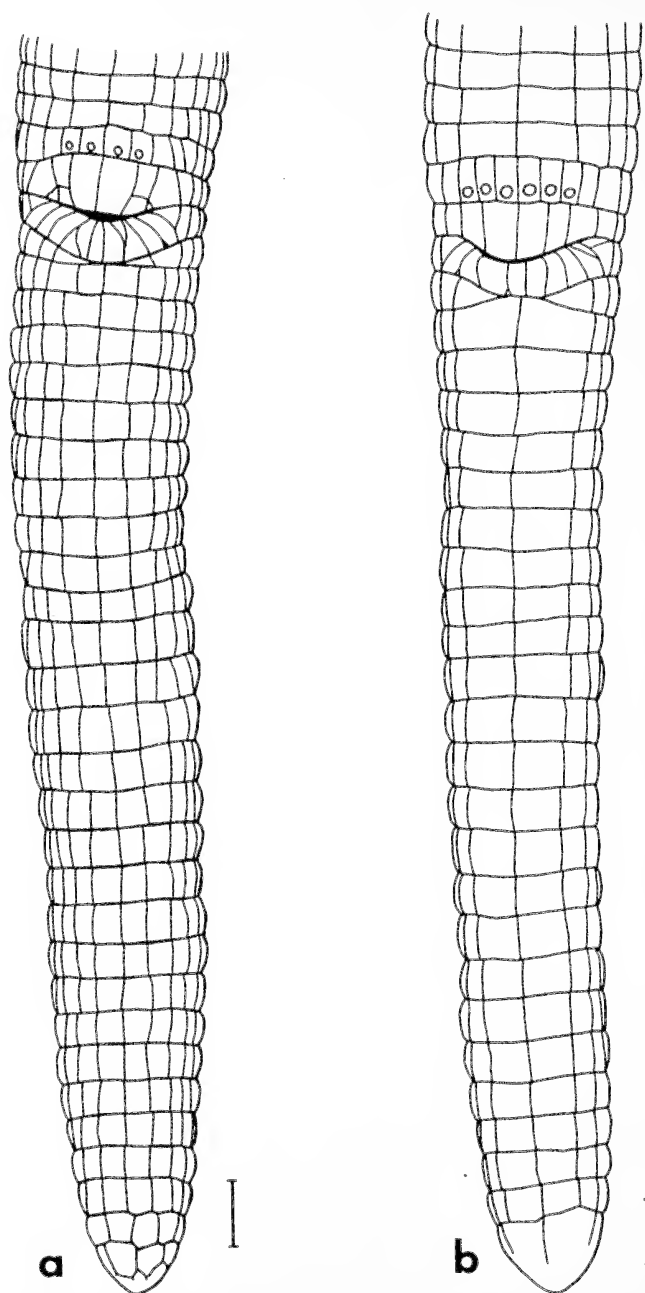


Fig. 9.—*Chirindia*. Ventral view of cloaca and tail. Line equals one mm to scale. Left, *C. langi*, TM 28,867. Right, *C. swynnertoni*, CM 61,808.

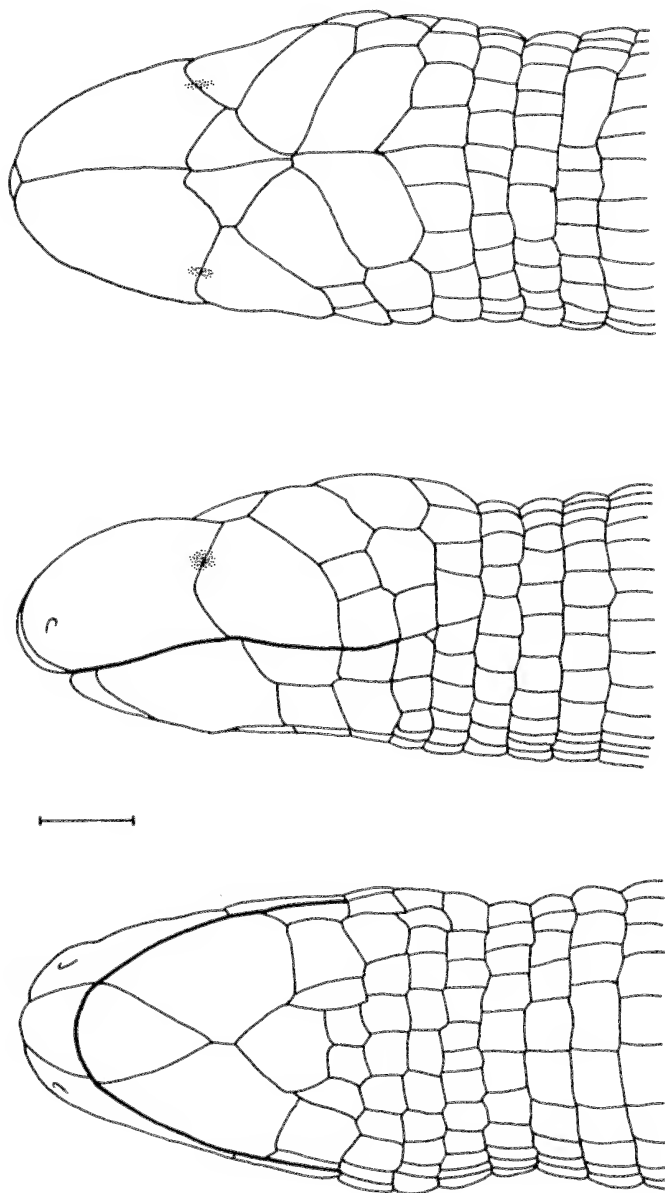


Fig. 10.—*Chirindia swynnertoni*. Dorsal (top), lateral (middle), and ventral (bottom) view of CM 61,805 from Haroni Forest to show segment proportions. The line equals one mm to scale.

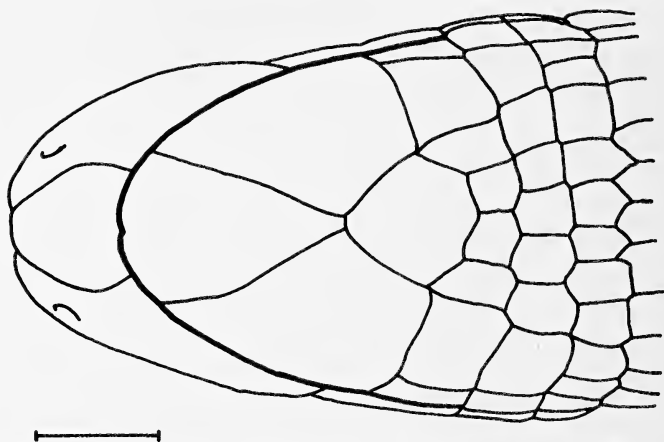


Fig. 11.—*Chirindia swynnertoni*. Ventral view of the head of CM 61,803 from Haroni Forest to show a specimen with the first infralabials separated by mental-postgenial contact.

small temporal shields. There is frequently some irregular enlargement of the mid-dorsal segments of the first body row posterior to the parietals.

The anterior post-supralabial is usually larger than the posterior one. They are occasionally fused.

Segmentation of the Lower Jaw.—The large, almost kite-shaped mental is wedged between the enormous first infralabials, by far the largest segments of the lower jaw, which are often in contact with each other. Other specimens, however, show the posterior tip of the mental in contact with the enlarged submedial segment of the first "postgenial" row. The latter may have one to four segments and the second row three to five (a single row is rare in *C. swynnertoni*), in addition to a row of six to 11 "postmalars," comprising the ventral segments of the first body annulus. In contrast, the types of *C. orientalis* always show two enlarged segments in series, the first corresponding to the postmental. The second is generally flanked by several smaller segments and is clearly equivalent to an enlarged medial segment of the first postgenial row. Comparison suggests that it is the second, and not the first, that is retained in *C. swynnertoni* and *C. langi*; hence, these species have lost the postgenial.

Body Proportions and Size.—Sexual dimorphism in both total length and relative tail length has been demonstrated for the Tanzanian forms *C. rondoensis* and *C. ewerbecki nanguruwensis* (Gans and Rhodes, 1967), but no consistent sexual dimorphism in these characters is discernible in the southern populations of *Chirindia* (Fig. 3).

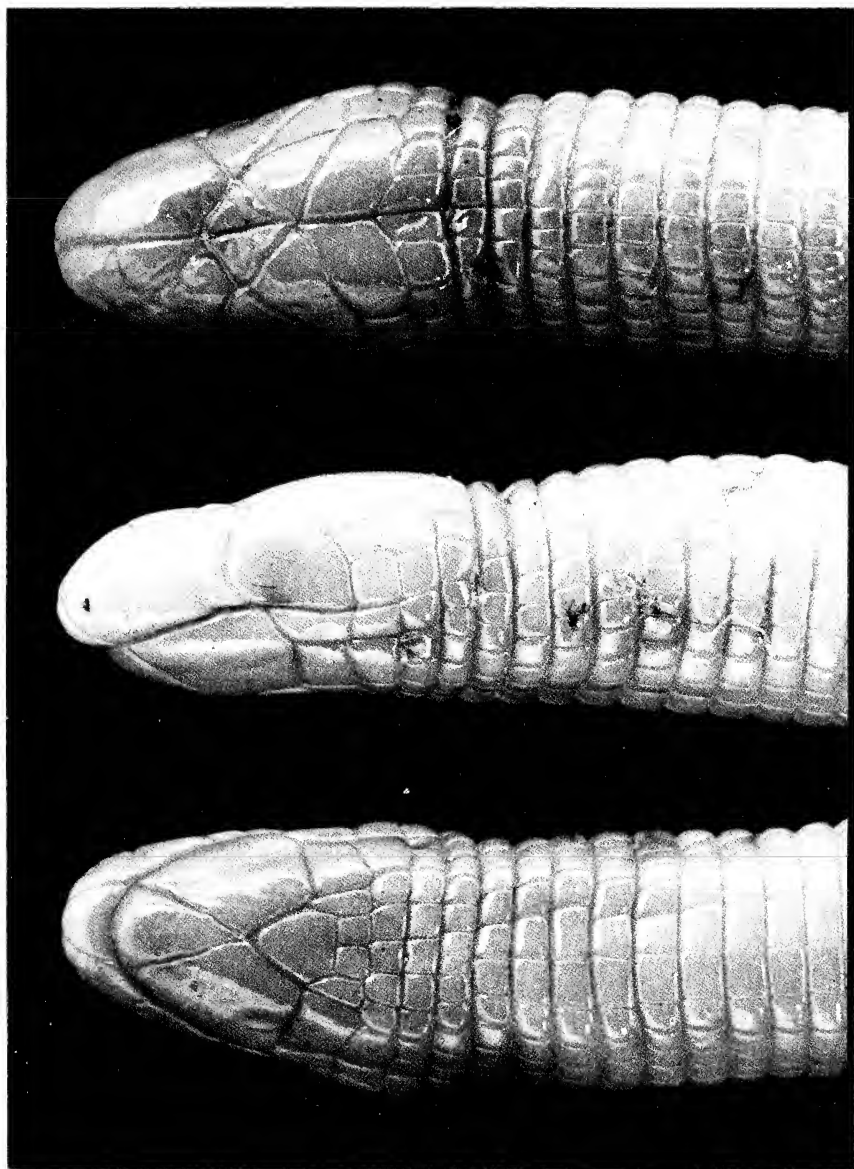


Fig. 12.—*Chirindia swynnertoni*. Dorsal, lateral, and ventral views of the head of CM 61,805 to show curvature and pigmentation of segments.

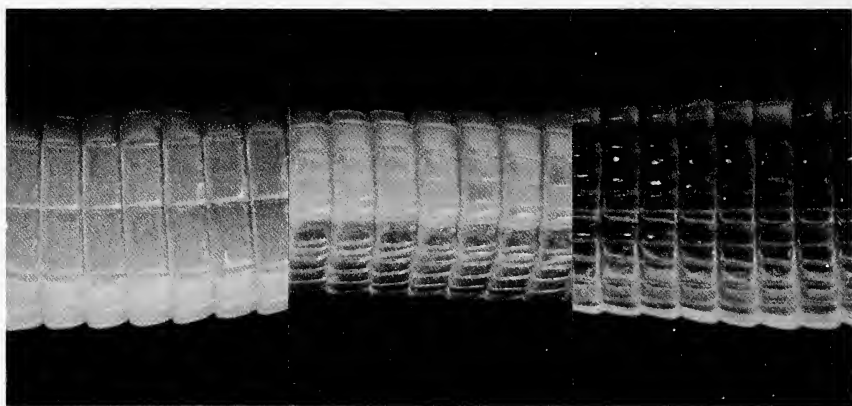


Fig. 13.—*Chirindia swynnertoni*. Dorsal (left), lateral (middle), and ventral (right) views of midbody UM 27,692 to show pigmentation and segment proportions.

Pores.—Precloacal pores are present in males only. There are usually four (rarely five or six) pores in *C. langi* and six in *C. swynnertoni* (seven in UM 29108; two in UM 27695).

Cloacal Shields.—There are usually six precloacal shields, rarely seven or eight, but the type of *C. swynnertoni* has only two. Postcloacal shields number six to 13.

Coloration.—*Chirindia langi* lacks pigmentation. *Chirindia swynnertoni* may be unpigmented anteriorly, but the posterior dorsals are always more or less pigmented. Generally most dorsal segments are mottled light to dark brown, with scattered unpigmented segments. Some pigmented segments occur ventral to lateral sulci. The tail is usually strongly pigmented, the tip being the darkest area on the body. One specimen (UM 27,606) is unusual in having the top of the head strongly pigmented. Another specimen (UM 20,666) has transverse bands of unpigmented dorsal segments.

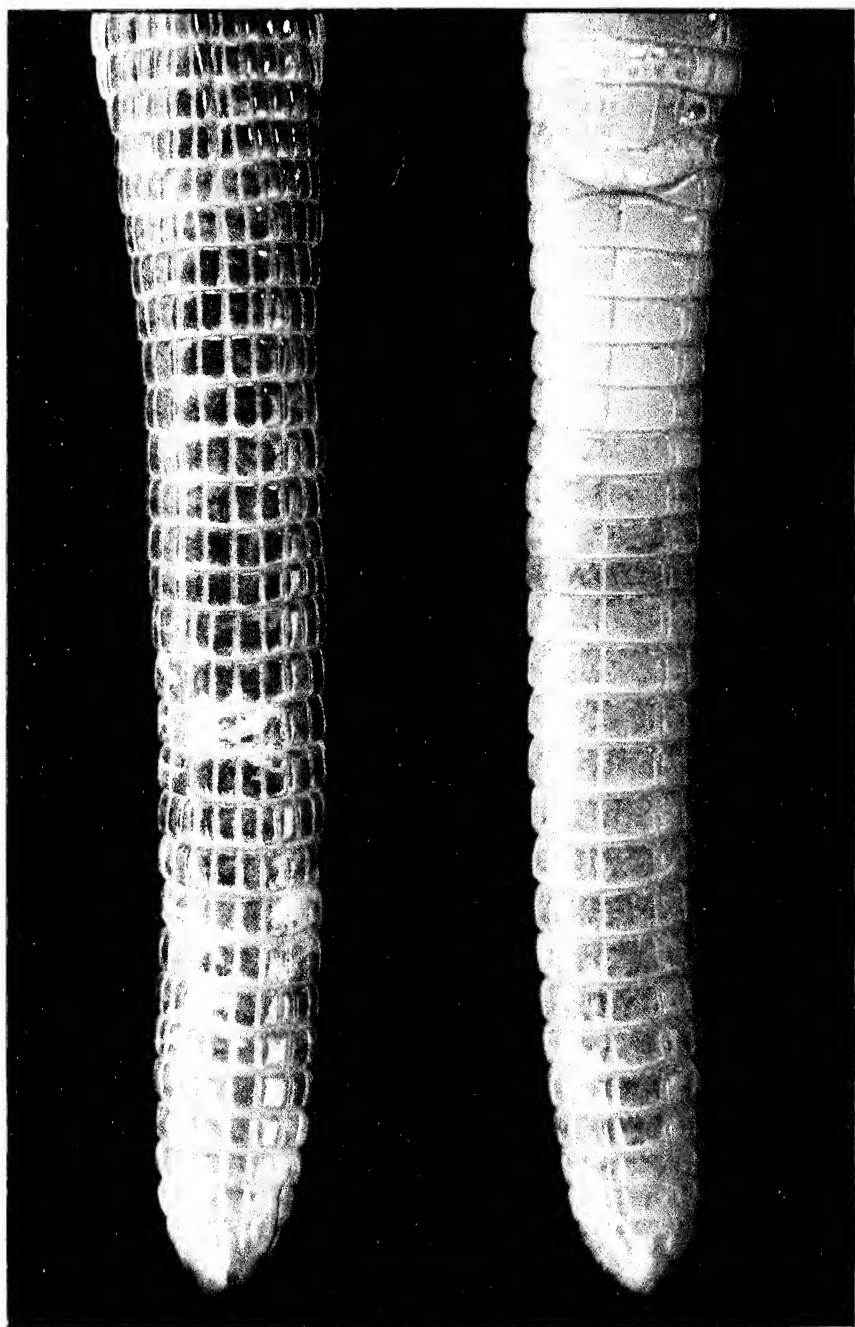
TAXONOMY

The characters used to separate *C. bushbyi* Cott from *C. swynnertoni* Boulenger (temporals only in point contact and minor differences in counts of body and caudal annuli) were found to fall within the range of variation of the latter taxon when adequate series became available.

The only southern population of *Chirindia* of doubtful status is rep-

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Fig. 14.—*Chirindia swynnertoni*. Dorsal (left) and ventral (right) views of cloaca and tail of UM 27,692 to show proportions and pigmentation.



resented by the unique specimen of *C. langi* from Wylie's Poort. It is distinguished from the "Kruger/Pafuri" populations by its low count of body annuli (262). It also has a high count of midbody segments (16/18) and six precloacal pores instead of the usual four found in *C. langi*. However, it is possible that intermediate populations of *C. langi* will be found in the northeastern Transvaal, so it seems premature to give nomenclatural recognition to the Wylie's Poort specimen.

KEY TO THE GENUS *CHIRINDIA*

- 1a. Supralabials three; total segments in a midbody annulus usually 28 or more 2
- 1b. Supralabials two; total segments in a midbody annulus usually 20 to 26. 3
- 2a. A discrete ocular present; body annuli 266 to 272; usually five or six precloacal pores in males *C. mpwapwaensis*
- 2b. Ocular usually fused with second supralabial; body annuli usually 277 to 303; usually four precloacal pores in males *C. langi*
- 3a. Parietals not in lateral contact with post-supralabials; snout rounded .. 4
- 3b. Parietals laterally in contact with post-supralabials; snout pointed 5
- 4a. Postmental present, tail shorter *C. orientalis*
- 4b. Postmental lacking, tail longer *C. swynnertoni*
- 5a. Body annuli 200 to 256; 10 segments in a midbody annulus ventral to the lateral sulci; usually 22 to 25 caudal segments *C. rondoensis*
- 5b. Body annuli 253 to 282; 12 segments in a midbody annulus ventral to the lateral sulci 6
- 6a. Usually 12, sometimes (<15%) 10 segments in a midbody annulus dorsal to the lateral sulci; usually 26 to 28 caudal annuli . *C. ewerbecki ewerbecki*
- 6b. Ten segments in a midbody annulus dorsal to the lateral sulci; usually 23 to 25 caudal annuli *C. ewerbecki nanguruwensis*

SUMMARY OF SPECIES

Chirindia langi FitzSimons

Chirindia langi FitzSimons (1939a: 8, Figs. 5–8).

Type locality.—"Punda Maria (=Punda Milia), northeastern Transvaal."

Holotype.—TM 19,197.

Paratype.—TM 19,198.

Locality Records.—*Transvaal*: Wylie's Poort, CM 61799; near Makwene Hill, TM 32955–32956; Kruger National Park ("K.N.P.") below western boundary north of Mutale River, CG (2 specimens), NKW 306 (10 specimens), 307A–307F, 308A–308C, UM 31,813; K.N.P. western boundary between Luvuvhu and Mutale Rivers, NKW 309A–309J, UM 31814; Bobomene, NKW 217; Hape Pan, Pafuri (Pienaar, 1966), CG 4476–4477, NKW 123, 154A–154D, NMP 1478A–1478C, TM 26317; Pafuri (Pienaar, 1966), TM 28866–28868; Papkuilfontein to Luvuvhu River, NKW 145A–145C; Mahembane to Magovane (Pienaar, 1966), NKW 207A–207D; Punda Maria (FitzSimons, 1939a,

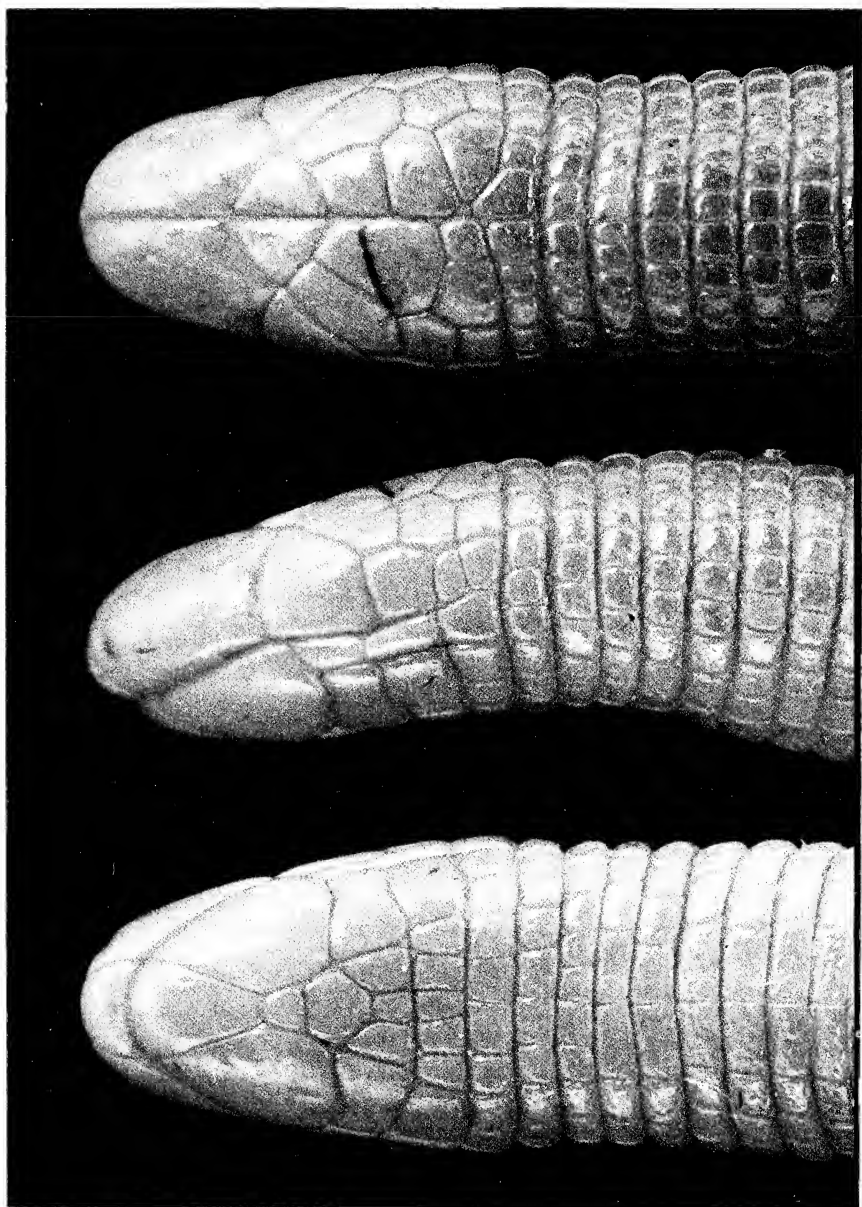


Fig. 15.—*Chirindia orientalis*. Dorsal, lateral, and ventral views of the head of the holotype ZMU 22,407 to show proportions, curvature, and pigmentation.

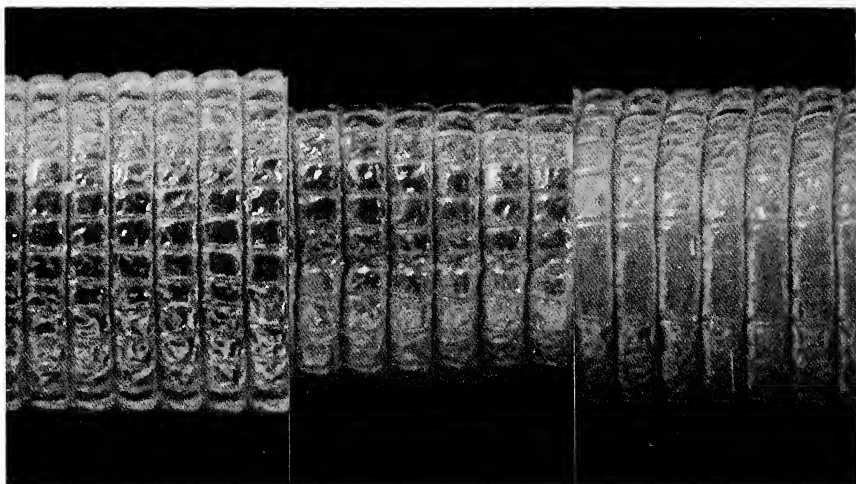


Fig. 16.—*Chirindia orientalis*. Dorsal (left), lateral (middle), and ventral (right) views of midbody of ZMU 22,407 to show pigmentation and segment proportions.

1943; Loveridge, 1941; Pienaar, 1966), NKW 54, 103, TM 19197 (holotype), 19,198 (paratype); K.N.P. eastern boundary between Pafuri and Shilahladonga Spruit, NKW 323, 328, TM 28, 869; K.N.P. eastern boundary between Nyandu sandveld and Beacon 7, CM 61,798, UM 31,585; K.N.P., CG 4519–4520.

***Chirindia swynnertoni* Boulenger**

Chirindia swynnertoni Boulenger (1907: 48, figs.).

Type locality.—"Chirinda Forest, southeast Mashonaland."

Holotype.—BM 1946.8.2.36.

Chirindia bushbyi Cott (1934: 158, Fig. 2), new synonym.

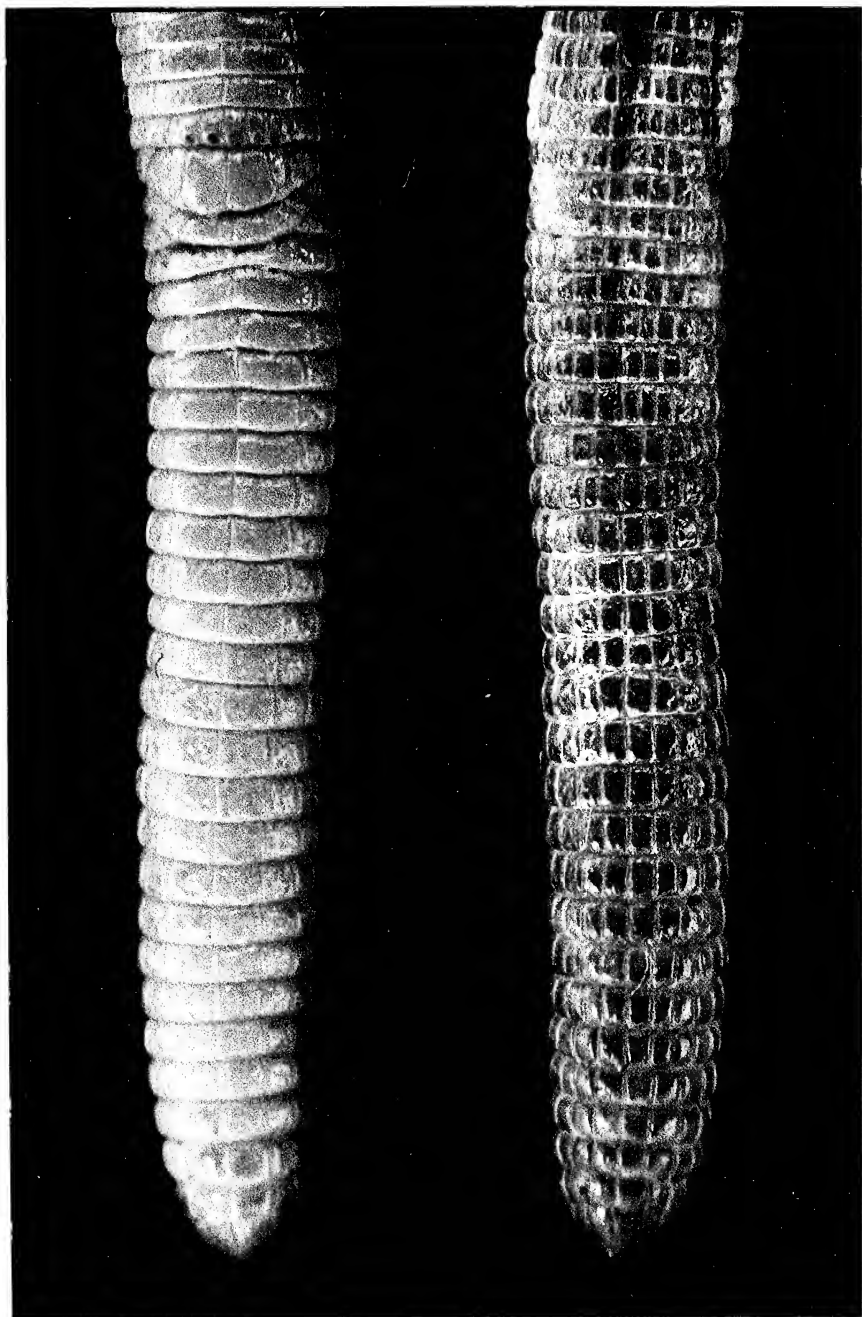
Type locality.—"Amatongas," Mozambique.

Holotype.—BM 1946.8.2.5.

Locality Records.—*Rhodesia*: Chirinda Forest (Boulenger, 1907; FitzSimons, 1939b, 1943; Loveridge, 1941; Broadley, 1966); BM 1946.8.2.36 (holotype *swynnertoni*); Haroni Forest, CM 61,803–61,805, UM 19,200, 20,677–20,679, 20,681–20,684, 20,687, 20,818–20,819; Makurupini Valley, CM 61,800–61,802, UM 20,666–20,674, 20,689–20,691.

→

Fig. 17.—*Chirindia orientalis*. Dorsal (right) and ventral (left) views of cloaca and tail of ZMU 22,407.



Mozambique: 25 km SE of Vila de Manica (Broadley, 1966), CG 4031, 4033, 4035, 4037–4038, UM 3565–3567, 11,742, 20,333–20,336; Mavita, UM 11,593; Espungabera (Buzi Bridge), UM 27,789–27,790; 25 km SE of Vila Paiva de Andrada (Broadley, 1966), UM 10,034; Amatongas (Cott, 1934; Loveridge, 1941; FitzSimons, 1943; Broadley, 1966), BM 1946.8.2.5 (holotype *bushbyi*); 25 km N of Lower Revue bridge, UM 27,646; Lower Revue bridge, UM 27,606; Amamba, CM 61,807–61,809, UM 27,681–27,690, 27,694–27,695; near Chibabava, CM 61,810, UM 27,768; Canganetole, CM 61,813–61,815, UM 29,108–29,109, 29,112–29,114; Chitengo Camp, CG 4018; Muda-Lamego (Broadley, 1966), UM 6081–6082; Dondo Forest, CM 61,806, UM 22,028–22,030, 22,032–22,033; Manga, CM 61,811–61,812, UM 29,096–29,098, 29,101.

BIOLOGICAL MISCELLANY

Chromosomes.—Huang and Gans (1971) note that *Chirindia swynnertoni* (as “*C. species*”) and *C. langi* both have six pairs of metacentric M and, respectively, nine to 10 and nine to 11 pairs of m chromosomes. Some of the m chromosomes of *Chirindia swynnertoni* appear to be metacentric.

Hearing.—The ear and hearing of *Chirindia langi* have been discussed by Gans and Wever (1972) and Wever and Gans (1973).

Breeding.—A *C. swynnertoni* from Dondo Forest contained an egg measuring 22 by 3 mm on 14 December.

Predators.—Although the type-specimen of *C. swynnertoni* was recovered from the crop of a kingfisher, *Halcyon albiventris* (FitzSimons, 1939), the most important predator on this small amphisbaenian seems to be the snake *Cryptolycus nanus*, which was originally described from 11 specimens collected from an oil-pipeline trench, at Xiluvo and Muda-Lamego in Mozambique (Broadley, 1968). Two *Chirindia* were also collected at the latter locality.

In July 1969, the authors collected additional specimens of both *Cryptolycus* and *Chirindia* at two more localities—25 km SE of Vila de Manica and near Chitengo Camp at the Gorongosa National Park. The *Cryptolycus* from the latter locality contained a partially digested *Chirindia*.

In August 1969, a Schools Exploration Society Expedition collected 29 *Chirindia* and one *Cryptolycus* in the Makurupini Valley on the Rhodesia-Mozambique border. This *Cryptolycus* had two *Chirindia* in its stomach.

The distribution of *Cryptolycus nanus* seems to coincide with that of *Chirindia swynnertoni*, and so far there is no evidence that it eats anything other than *Chirindia*. This monotypic genus differs from typical wolf snakes of the genus *Lycophidion* in the reduction in size of its head, number of labial shields, and number of teeth on all dentigerous bones. It is apparently in the process of modification for a fossorial existence and a diet of *Chirindia*. The numerous species of *Lycophidion* are essentially skink-eaters.

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ARTICLE 4

ANATOMY AND RELATIONSHIPS OF THE FAMILY PHLEGETHONTIIDAE (AMPHIBIA, AÏSTOPODA)

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ABSTRACT

The cranial and cervical osteology of the middle Pennsylvanian aïstopod amphibian *Phlegethontia linearis* Cope, from Linton, Ohio, is described. *Aornerpeton mazonense* (Gregory), new genus, and *Sillerpeton permianum*, new genus and species, are compared and contrasted with *P. linearis* in endocranial structure and in the functional anatomy of their feeding mechanisms.

The feeding mechanism of *Phlegethontia linearis* is investigated. It displays cranial kinesis with unilateral jaw movements, in a manner analogous to that of snakes. The articulations of upper and lower jaws indicate a capacity to ingest large prey items, the reduction of the gastralia may have facilitated sufficient ventral distention of the body to compensate for a lack of lateral palatal mobility.

The Phlegethontiidae and Ophiderpetontidae show widely divergent cranial specializations but are related on the basis of their common and uniquely derived postcranial characters. The Aïstopoda cannot be derived from or closely related to any presently known amphibian group.

INTRODUCTION

Two genera have been included within the aïstopod amphibian family Phlegethontiidae of Cope—*Dolichosoma* Huxley, 1867, and *Phlegethontia* Cope, 1871—the former from the early Pennsylvanian of Europe, the latter from the middle Pennsylvanian to early Permian of

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the United States. One other family is included in the Aïstopoda, the Ophiderpetontidae. The Ophiderpetontidae contains only the genus *Ophiderpeton*, which ranges from the early Mississippian of Scotland to the middle Pennsylvanian of the United States (Baird, 1964).

Members of the Aïstopoda are snakelike, lack either limbs or girdles, and possess holospondylous centra with intravertebral foramina and k-shaped ribs. *Ophiderpeton* has a dense dorsal and lateral covering of osteoderms on the head and body and tightly-fitting gastralialia. The Phlegethontiidae lack dorsal and lateral osteoderms and have very thin, widely separated gastralialia.

Dolichosoma emersoni, the type species of *Dolichosoma*, is indistinguishable from *Ophiderpeton* (Bossy, personal communication). A second nominal species, *D. longissima* Fitch, 1875, is indistinguishable from *Phlegethontia linearis* Cope, 1871, the type species of *Phlegethontia* (McGinnis, 1967). McGinnis unfortunately used an incorrect combination, *P. longissima* (McGinnis, 1967).

P. linearis is known from the late Westphalian D of the type locality, Linton, Ohio, and from Nýřany, Czechoslovakia, the type locality of *Dolichosoma longissima*. Gregory (1948) named and superbly described a second species, *P. mazonensis*, from the early Westphalian D of Mazon Creek, Illinois. Turnbull and Turnbull (1955) added some information on skull morphology to the description of *P. mazonensis* on the basis of a second specimen. McGinnis (1967) described a phlegethontiid braincase from the early Permian of Fort Sill, Oklahoma. McGinnis (1967) synonymized all *Phlegethontia* into one species, failing to deal adequately with the limited, often crushed specimens of *P. linearis* from Linton, Ohio, and not taking into account the differences between *P. mazonensis* and the Fort Sill braincase.

Recent work at the Linton locality by Carnegie Museum of Natural History field parties has produced two additional specimens of *Phlegethontia*. One specimen, Carnegie Museum (CM) 23,053 is a well preserved skull over 27 mm in length and the other, CM 23,056, is a small individual with well preserved otic region and anterior vertebrae. Investigation of these specimens has clarified several problems in morphology, and comparison with other phlegethontiid material has resulted in new understanding of the systematics, form, and function of the members of this highly specialized family of amphibians.

The Phlegethontiidae are specialized predators with cranial kinesis and, at least in *P. linearis*, a capability for unilateral jaw motions analogous to that of snakes. Strong morphologic differences justify generic separation of *P. linearis*, *P. mazonensis*, and the Fort Sill specimen as well. These differences indicate a striking degree of functional diversification within the group and isolate them from any other known amphibian.

ACKNOWLEDGMENTS

Many thanks to Helen McGinnis for her extensive discussions and loan of photographs. Paul Harris and the Field Museum of Natural History have graciously permitted me to reproduce the photograph of FM-MCP 501. The invaluable assistance, advice, latex peels, and finally the goading of Donald Baird cannot be adequately repaid, and his expertise in naming has produced one of the new names below. Kathleen Hahn Bossy has freely discussed her work in progress. To the many persons in my field parties to Linton, and particularly to Donald Mullenau, who found CM 23,053, my deepest gratitude.

Abbreviations.—AMNH, American Museum of Natural History, New York; CM, Carnegie Museum of Natural History, Pittsburgh, Pennsylvania; MCZ, Museum of Comparative Zoology, Harvard University, Cambridge, Massachusetts; UCMP, University of California Museum of Paleontology, Berkeley, California; USNM, United States National Museum, Washington, D.C.; FM, Field Museum of Natural History, Chicago, Illinois.

SYSTEMATIC PALEONTOLOGY

Order Aïstopoda

Family Phlegethontiidae Cope

Phlegethontia linearis Cope, 1871

Holotype.—AMNH 6966 and counterpart 6886, from the Freeport Formation, Allegheny Group, Westphalian D, of Linton, Jefferson Co., Ohio.

Synonymy.—*Dolichosoma longissima* Fritsch, 1875.

Diagnosis.—Phlegethontiid with separate parietals, supraoccipital and tabulars composing roof of braincase; prominent sagittal crest on supraoccipital separating extensive temporal fossae posterior to pineal opening; long sphenethmoid; single, elongate, anterior foramen for cranial nerves 5 and 7; one pair of palato-braincase processes, the *tubera basisphenoidales* of Gregory (1948); rear margin of palatoquadrate vertical; ribs dorsally expanded, articulated to each other anteriorly.

Occurrence.—The Westphalian D, middle Pennsylvanian of Linton, Ohio, and Nýřany, Bohemia, Czechoslovakia.

Description

Growth.—The contention by McGinnis (1967) that the length of the snout of *Phlegethontia linearis* exhibits positive allometry relative to the skull length is not sustained either by her graph (McGinnis, 1967: Fig. 4) or by any other measurements. Within the limits of a statistically very small sample, size ratios for all measured length parameters are extremely close. Examination of specimens shows that apparent relative elongation of the snout can be accounted for by two factors—postmortem deformation of the anterior part of the premaxilla, and postmortem anterior dislocation of the premaxilla-nasal complex.

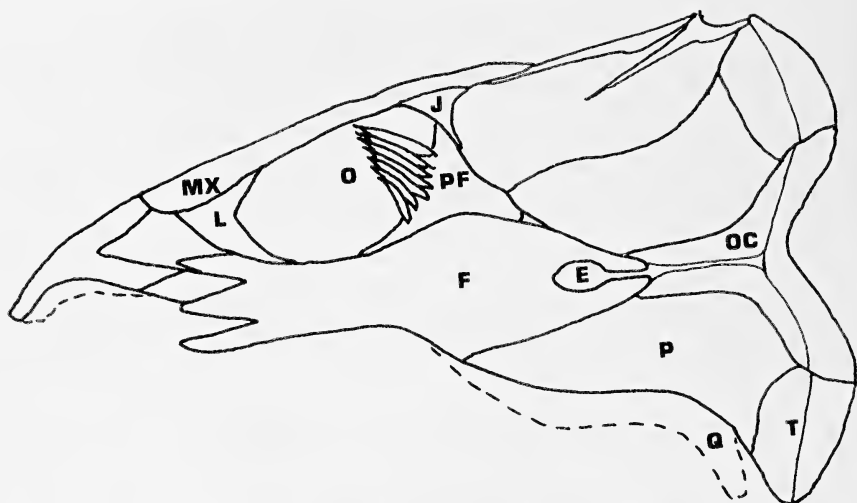


Fig. 1.—*Phlegethontia linearis*, skull roof in dorsal view. After AMNH 6966, 6886, 2564, MCZ 2038, CM 23,053. E, pineal foramen; F, frontal; J, jugal; L, lacrimal; MX, maxilla; O, orbital osteodermi; OC, occipital; P, parietal; PF, postfrontal; Q, pterygoquadrate; T, tabular.

USNM 4484, which McGinnis (1967:36) contends may be a separate species, has been subject to crushing from above and postmortem anterior dislocation and deformation. There are no reasons to believe that this specimen represents a separate species.

There is noticeable relative elongation of the circumpineal prongs of the frontal with increased size in the few specimens that display this region well. The sagittal crest is well developed on even the smallest specimen of *P. linearis*, MCZ 2038, braincase length 3.5 mm. This contrasts strongly with the lack of a sagittal crest in the type specimen of *P. mazonensis*, USNM 17,097, which is 4 mm in braincase length.

Osteology.—Examination of latex peels of all known Linton *Phlegethontia* skulls has made it possible to prepare a refined restoration of the skull (Figs. 1–2). All details have been verified in at least two specimens except for the tympanic bones. Names of the elements follow Gregory (1948) where possible.

The premaxilla has a strong ascending process, firmly joined at its dorsal margin to the nasal, and separated from its opposite in the mid-line by the median prong of the frontal. The facial portion of the premaxilla abuts loosely against the anterior end of the maxilla. The lacrimal abuts loosely against the edge of the lateral prong of the frontal (=fused prefrontal?) and forms the entire anterior border of the orbit. It ends ventrally in a concave face far too thick to have served merely as an

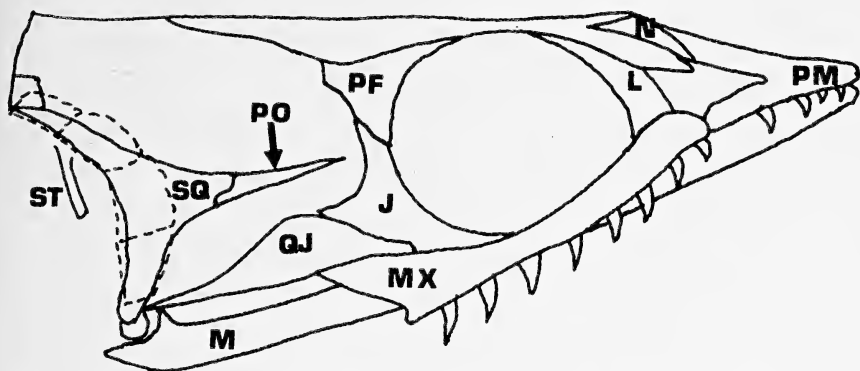


Fig. 2.—*Phlegethontia linearis*, skull restored in lateral view, tympanics dashed to show squamosal. J, jugal; L, lacrimal; M, mandible; MX, maxilla; N, nasal; PF, postfrontal; PM, premaxilla; PO, postorbital; QJ, quadratojugal; SQ, squamosal; ST, stapes.

articulation for the relatively thin, slightly convex anterior expansion of the maxilla. The maxilla has a slightly wavy but smooth dorsal surface, onto which fit the jugal and quadratojugal. The posterior border of the maxilla is slightly thickened, and the maxilla deepens markedly posteriorly.

The postfrontal (Figs. 2, 3) fits against the postorbital process, tapers to a point anterodorsally, and is thick at its posterodorsal end. The ventral extension is narrow, relatively thick, and bears a shallow vertical groove ventrolaterally. The dorsal half of the bone is flat in lateral aspect in AMNH 2564, and well rounded in the type specimen, AMNH 6966, but in each the ventral half is overlain by the jugal in a loose, sliding articulation that invariably hides the ventral end of the postfrontal. The jugal forms the posteroventral quarter of the orbital margin, lying against the dorsal margin of the maxilla and the anterodorsal margin of the quadratojugal. The quadratojugal is long, thinning to a feather edge dorsally except where it abuts against the jugal. It has a slightly wavy anteroventral border, which evidently fits the posterodorsal edge of the maxilla. The quadratojugal is rarely found articulated with other bones.

The squamosal complex is composed of the wedge-shaped postorbital which fits like a hinged spike onto the short anterior process of the thin, curved squamosal, and a series of four thin, flat, scale-like tympanic elements, which lie lateral to the ascending portion of the squamosal. The posterodorsal end of the squamosal contacts the posterolateral (tabular) corner of the braincase, and the ventral end contacts the quadrate region of the pterygoquadrate.

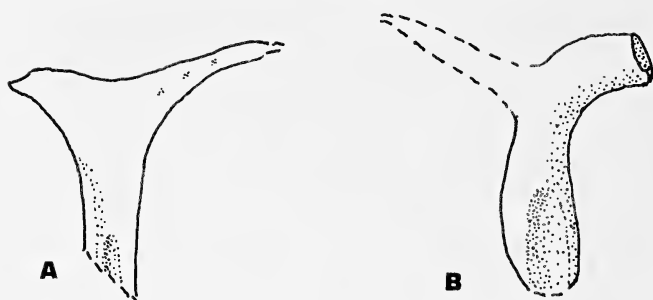


Fig. 3.—*Phlegethontia linearis*, postfrontals. A, AMNH 2564, B, AMNH 6966. Scale is 1 mm.

Several specimens, including MCZ 2038 (McGinnis, 1967: Fig. 2) have more than six thin, long, cranial osteoderms inclined anteroven- trally along the posterior border of the orbit anterior to the postfrontal and jugal (Fig. 1). These elements were incorrectly identified as sclerotics in MCZ 2038 and the Mazon Creek phlegethontiid (Gregory, 1948). Sclerotics are preserved in CM 23,053.

The endocranium of *Phlegethontia linearis* consists of three closely sutured components—the frontal, the sphenethmoid, and the braincase. The frontal bears descending flanges on the ventral surface in the orbital region to which the sphenethmoid is sutured, and lies over a dorsal emargination of the braincase in the pineal region.

The sphenethmoid, a large, V-shaped ossification in transverse section, meets the braincase at approximately mid-orbit, forming the greater part of the interorbital septum and the midline of the roof of the mouth. It overlaps the anterior end of the cultriform process postero- ventrally. The foramen for the optic nerve is located at the junction of sphenethmoid and braincase (Fig. 4). The olfactory nerves pass dor- sally between the branches of the V to emerge at the anterior end of the element, where they are divided by a descending medial vertical sep- tum from the preorbital portion of the frontal. This septum decreases in depth anteriorly until it vanishes at the anterior end of the central prong of the frontal.

The braincase consists of the following elements: distinct parietals dorsolaterally (Fig. 1), flooring the extensive temporal fossa; supraoc- cipital ridge dorsomedially, supporting the sagittal crest and not sepa- rate from the remainder of the occipital and its sharp occipital crests; small, square tabulars supporting the lateral extensions of the occipital

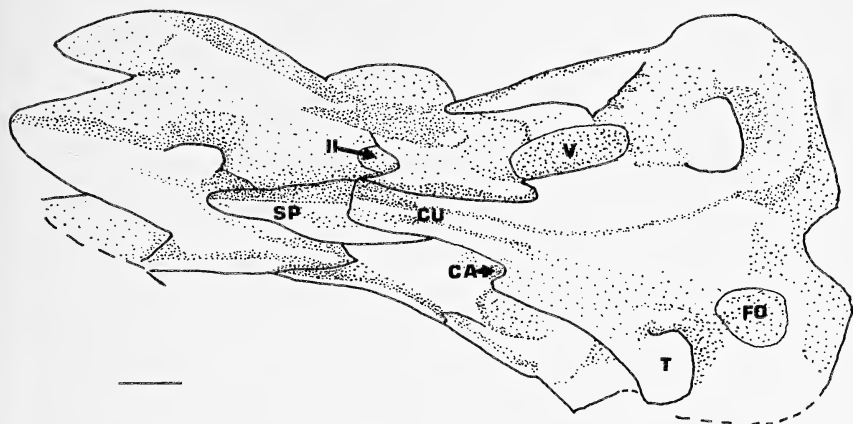


Fig. 4.—*Phlegethontia linearis*, MCZ 2334, braincase in ventral view. Scale is 1 mm. CA, carotid arterial foramen; CU, cultriform process; FO, fenestra ovalis; SP, sphenethmoid; T, *tuber basisphenoidalis*; II, optic foramen; V, foramen for nerves 5 and 7.

crests; a one piece ventral element. The braincase is structurally a single unit distinct from the frontal-sphenethmoid complex. The braincase in ventral view (Fig. 4) bears a short cultriform process, notched posteriorly for passage of the carotid arteries. Immediately posterodorsally is a single, elongate foramen for cranial nerves 5 and 7 (the "optic" foramen of Gregory, 1948). A broad anteroventrolaterally facing process, the *tuber basisphenoidalis* of Gregory (1948), projects from the ventrolateral margin of the braincase. The prominent fenestra ovalis is located near the rear margin of the braincase.

The anterodorsal margin of the braincase is deeply emarginate medially for reception of the frontal. The pineal opening is a keyhole-shaped opening in the posterior midline of the frontal. The parietals, separated in the midline, do not enclose the pineal opening anteriorly. The braincase of *P. linearis* differs from the Fort Sill braincase in features such as the position, shape, and relative size of the *tubera basisphenoidales* and carotid and prootic foramina, and in having distinct dorsal ossifications (McGinnis, 1967: Fig. 5b, c, Pl. 1C). Far more substantial differences exist between *P. linearis* and *P. mazonensis*.

The palate in phlegethontiids is composed of an anterior or palatine portion and a separate posterior unit incorporating pterygoid, epipterygoid, and quadrate. Palatal elements were loosely articulated with the remainder of the cranial elements in all known specimens, the only discrete articulatory arrangements being between epipterygoid and basicranial processes such as the *tubera basisphenoidales*. The Fort Sill

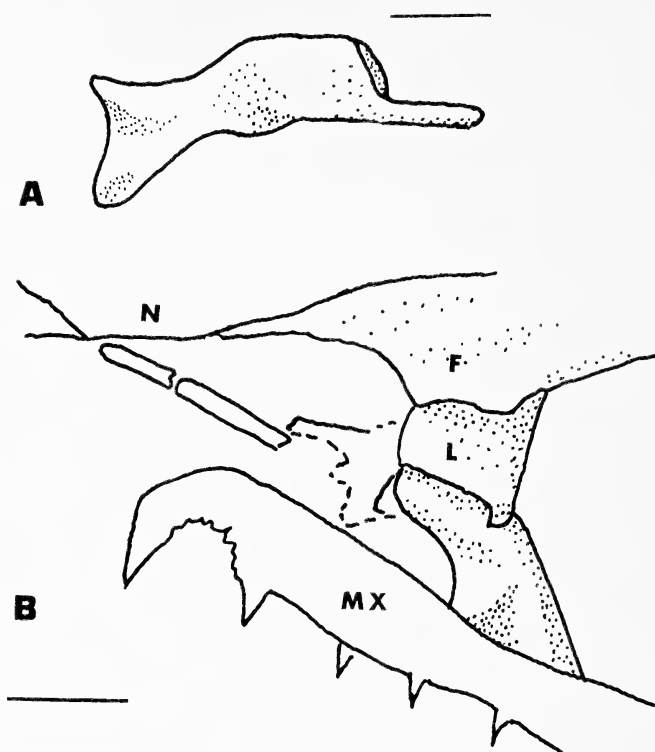


Fig. 5.—*Phlegethontia linearis*, A. MCZ 2301, ventral view of left anterior palatal element; anterior to left. Scale is 0.5 mm. B. Preorbital region of AMNH 6966. Scale is 1 mm. F, frontal; L, lacrimal; MX, maxilla; N, nasal.

braincase has a lateral facet, however, which probably articulated with the dorsal edge of the epipterygoid (McGinnis, 1967: Fig. 5).

The anterior palatal elements of *P. linearis* are known only from tantalizing fragments. An articulation between the pterygoquadrate and the anterior unit can be seen in CM 23,053. A thick, loose element in the snout of AMNH 6966 (Fig. 5B), associated with a thin anteriorly extending bar, seems to be a lateral view of an element seen in ventral view under the anterior end of the frontal of MCZ 2301 (Fig. 5A). This "palatine" is topographically associated with the anterior end of the maxilla and, through the anterior bar, with the posteroventral end of the premaxilla. No information is presently available on the anterior end of the palate of *P. mazonensis*.

The posterior, or pterygoquadrate, unit of *P. linearis* is a single element with no sutures, shaped approximately like a hatchet. It lies

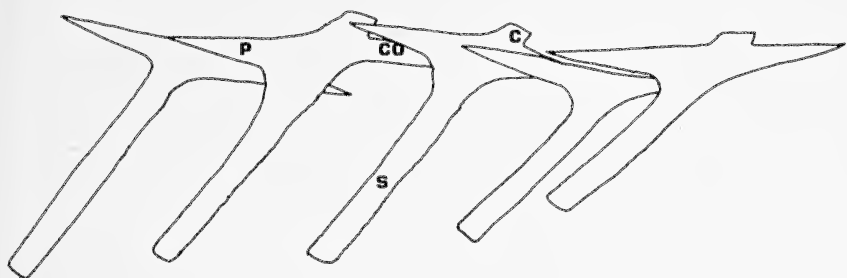


Fig. 6.—*Phlegethontia linearis*, AMNH 2564, first five ribs of right side, lateral view, C, capitulum; CO costal process; P, posteromesial process; S, shaft.

along the lateral surface of the braincase and extends anteriorly to an articulation at the level of the front of the orbit (Fig. 7). The posterior and dorsal margins are straight, and the quadrate condyle is a simple cylinder with a flared external edge. The pterygoid portion, the "handle" of the hatchet, is expanded only slightly at its anterior end.

Ribs.—The tetraradiate ribs of *Phlegethontia linearis* are difficult to visualize, and have been the subject of much debate (Baird, 1964). Baird's terminology for parts is used (Fig. 6). Significant differentiation of the first six ribs of the column exists, followed by gradual reduction of the specialized processes in the succeeding six ribs. The anterior ribs are each single-headed and bear a long, anteriorly directed costal process as well as a long, posteromesial process close to the capitulum. The first two ribs are short-shafted; the succeeding ribs have relatively uniform, longer shafts. The costal process of each tetraradiate rib extends ventral to the posteromesial process and mesial to the shaft of the rib anterior to it to form a tightly interlocked complex reminiscent of an avian rib cage. It seems incongruous to have the flexibility of single-headed ribs upon prominent transverse processes combined with tightly interwoven proximal regions of ribs, unless the system reflects the development of specialized cervical epaxial musculature associated with powerful support and movements of the head. Additional factors that may support this hypothesis are the following: the absence of ribs on the first two or three vertebrae; the strong transverse processes; the absence of occipital condyles; the well-defined and dorsomedially em-bayed occipital crest.

Aornerpeton, new genus

Type Species.—*Phlegethontia mazonensis* Gregory, 1948

Diagnosis.—Phlegethontiid with no separate dorsal ossifications in braincase; no sagittal crest; two pairs of palatobasal processes on

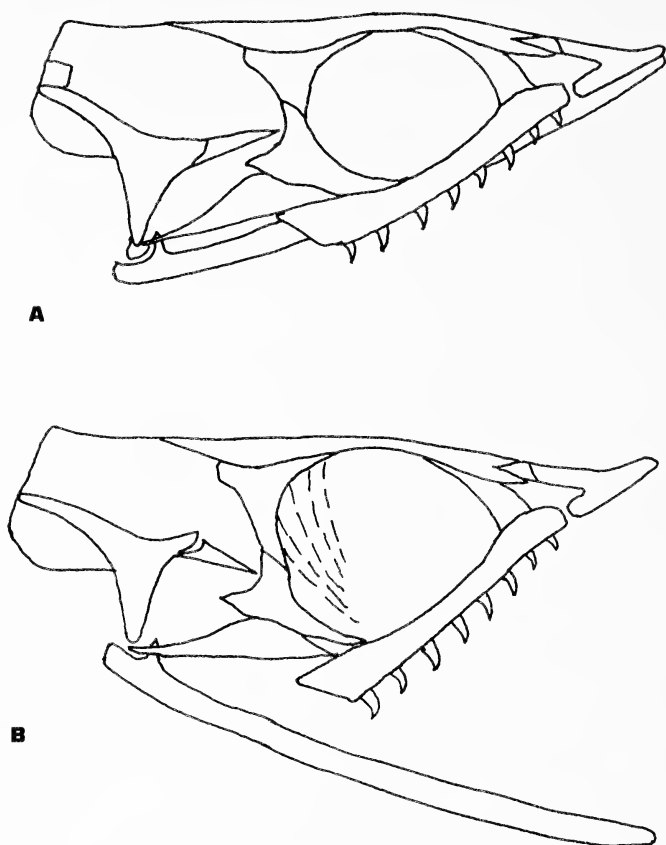


Fig. 7.—*Phlegethontia linearis*, jaw mechanics. See text for explanation.

braincase; cultriform process extending almost to anterior border of orbit; a lateral and an orbital foramen for branches of nerves 5 and 7; posterior margin of epipterygoid deeply notched dorsally lateral to lateral foramen for nerves 5 and 7; pterygoid flared anterolaterally; ribs very thin.

Derivation.—Named, as was *Phlegethontia*, for a watercourse in Hades—the river where no birds sing, according to Greek mythology.

***Aornerpeton mazonense* (Gregory, 1948)**

Holotype.—USNM 17079.

Referred Specimens.—FM-PR 281, FM-MCP 501, MCZ 2204.

Occurrence.—Francis Creek Shale, Carbondale Formation, Pennsylvanian, early Westphalian D of Grundy and Will counties, Illinois.

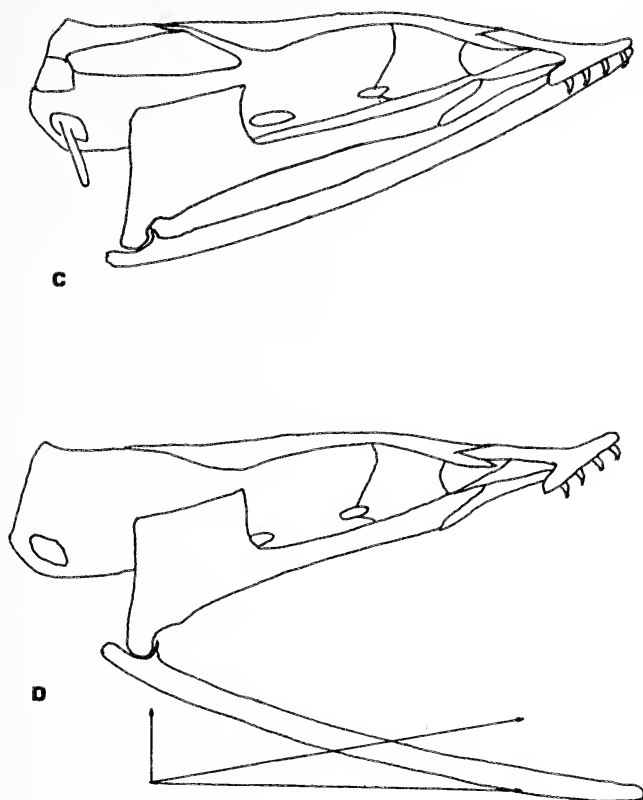


Fig. 7.—*Phlegethontia linearis*, jaw mechanics. See text for explanation.

Discussion.—Little can be added to Gregory's (1948) description of the type specimen, which has an excellent three dimensional skull lacking only the snout and several cheek bones. Characters used in the diagnosis of this genus demonstrate the great differences between *Phlegethontia* and *Aornerpeton*. Newly available material in private collections seems to bear a premaxilla of essentially similar shape and proportions to that of *Phlegethontia linearis*.

A few additional observations can be made on the known specimens of *Aornerpeton*. The lacrimal is thin laterally, but bears a mesial flange from its front edge. The elements identified as sclerotics by Gregory (1948) are relatively undisturbed orbital osteoderms. The postorbital process of USNM 17,079 is very slight and lacks a prominent groove for reception of a postfrontal in contrast to the condition in

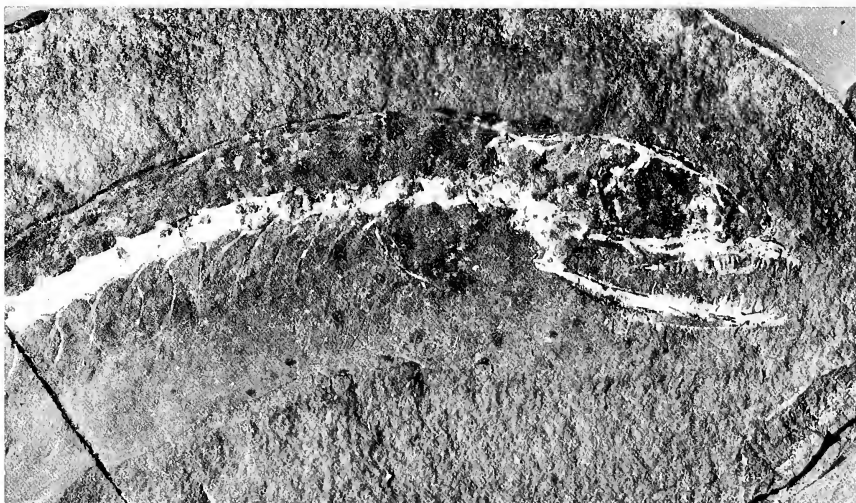


Fig. 8.—*Aornerpeton mazonense*, FM-MCP 501, Field Museum photograph. Paul Harris Collection.

Phlegethontia. A pineal opening is present in the specimen, evidently revealed by additional preparation after Gregory's description. The maxilla does not rise significantly posteriorly, unlike *Phlegethontia*, and does not extend past the rear of the orbit. The pterygoids of the type specimen (Fig. 10) are separate elements, which were originally sutured to the epipterygoids rather than fused as in the larger specimens of *Phlegethontia*. The posteroventromesial edges of the epipterygoids are somewhat upturned posterior and mesial to the *tubera basisphenoidales*. This would either effectively prevent significant palatal motion anteriorly and laterally or serve as ligamentous attachment areas for a palatobasal ligament. A prominent ligamentous scar is present on the posteroventral edge of the epipterygoid immediately in front of the quadrate process, evidently for a palatomandibular ligament that would insert anterior to the mandibular articulation. The ribs are long and very thin, although they seem to bear needle-like costal processes.

A specimen in the collection of Paul Harris (Field Museum photograph FM-MCP 501), retains a pigment pattern of three dark transverse bars at the dorsum of the neck, followed by one transverse row of dark spots on the dorsum per vertebral segment. The orbital region seems to have been all black including the top of the head, preceded by a few spots on the snout region. Smaller dark spots occur ventrally on the throat (Fig. 8, 9). The pattern of melanin markings is cryptic, disruptive

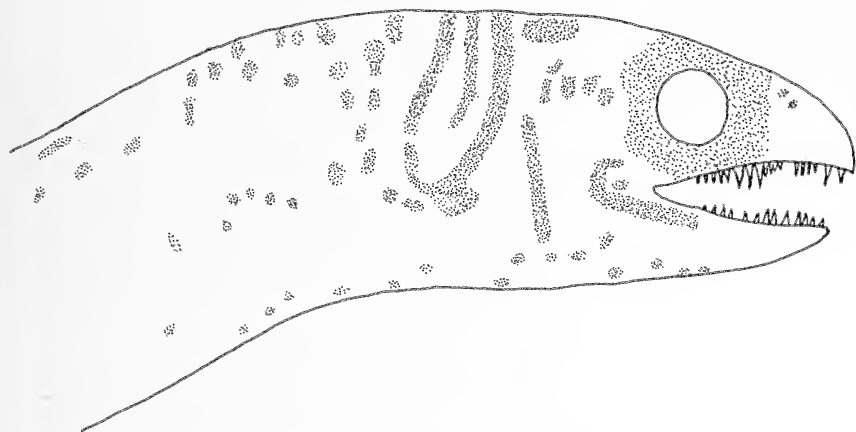


Fig. 9.—*Aornerpeton mazonense*, Color pattern and dentition. After FM-MCP 501.

coloration, comparable to that seen in juvenile *Coluber* or many other diurnal predaceous snakes (E. D. Brodie, Jr., personal communication).

Aornerpeton shows conspicuously derived character states over the condition seen in *Phlegethontia* in the degree of ossification of the braincase, the obliteration of the sagittal crest, the presence of a paroccipital process and the epipterygoid ridges associated with the *tubera basisphenoidales*, and the elongation of the cultriform process. Conditions, which seem to be plesiomorphic in *Aornerpeton*, include the presence of lateral and orbital foramina for nerves 5 and 7 (Thomson, 1965; Panchen, 1964), the notching of the margin of the epipterygoid, and the shape and independence of the pterygoid.

Sillerpeton, new genus

Type Species.—*Sillerpeton permianum*, new species.

Provisional Diagnosis.—Phlegethontiid with completely fused braincase; no sagittal crest; a fossa for articulation of the dorsal end of the epipterygoid and narrow vertical articular *tubera basisphenoidales* for palatal articulation; cultriform process not projecting beyond edge of braincase midorbitally; single, orbital foramen for cranial nerves 5 and 7.

Derivation.—Named for Fort Sill, Oklahoma.

Sillerpeton permianum, new species

Phlegethontia cf *P. linearis* (McGinnis, 1967, fig. 5)

Holotype.—UCMP 62,480, braincase.

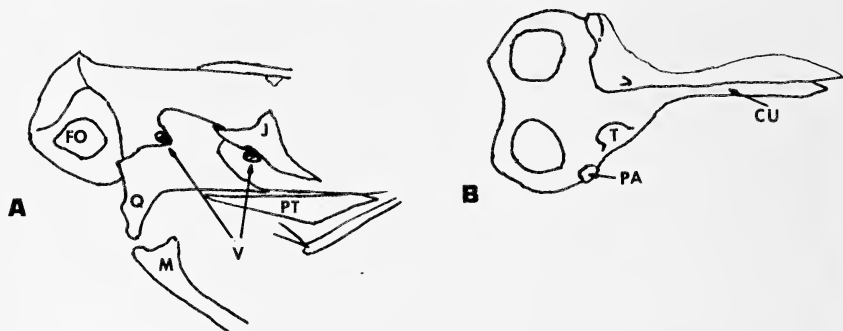


Fig. 10.—*Aornerpeton mazonense*, USNM 17,097 type. A. lateral view. B. ventral view, left side without palate; CU, cultriform process; FO, fenestra ovalis; J, jugal; M, mandible; PA, paraoccipital process; PT, pterygoid; Q, quadrate-epipterygoid; T, *tuber basiphenoidalis*; V, foramina for nerves 5 and 7.

Referred Specimens.—UCMP 62,580, braincase; UCMP 63,835, two fused vertebrae; UCMP 63,831, 63,832, 63,833, 63,834, YPM 3701, separate vertebrae. Collected by Frank E. Peabody and Wann Langston.

Diagnosis.—Same as for the genus, only known species.

Occurrence.—"Fissure deposit in the Arbuckle limestone at the Dolese Brothers Limestone Quarry, approximately 6 mi north of Fort Sill, in Sec. 31, T. 4N, R. 11W, Comanche Co., Oklahoma; University of California Museum of Paleontology Locality V5052. This locality is also known as Richard's Spur. The site has since been obliterated by quarrying operations, although bones may still be collected from other nearby fissure deposits."

"The braincase came from a block of material cemented together with calcium carbonate, collected from a vertical fissure in the Ordovician Arbuckle limestone by Frank E. Peabody in 1950. In his notes this fissure is designated as FEP 60A (for further description of the locality, see Peabody, 1961)" (McGinnis 1967).

Horizon.—Early Permian age, perhaps equivalent to the Arroyo formation, Lower Clear Fork Group of Texas (Olson, 1954).

FUNCTIONAL ANATOMY

The cranial elements of *Phlegethontia linearis* are grouped into the following functional units for subsequent discussion: snout; cheek; pterygoquadrate; palatine; endocranium; mandible.

Snout

The premaxilla, nasal, and prevomer constitute the snout. The premaxilla has a low anterior portion which curves around from the midline towards the ascending process, and bears a single line of well-spaced teeth along its ventrolateral margin. The posterior margin of the ascending process abuts against the nasal fitting into the notch between the median and lateral prongs of the frontal. Both bone junctions are narrow, smooth, rounded surfaces rather than sutures. The posterior process of the premaxilla presumably abuts against the maxilla, but there is no known line of fit in any specimen. The two premaxillae and nasals are separated from each other posteriorly in the dorsal midline by the median prong of the frontal. The prevomer is unknown. The anterior end of the premaxilla is expanded into a thin, rounded, ventrally concave cup, considerably wider than the dorsal surface of the ascending process, and not apparently sutured to the opposite premaxilla.

The two sides of the snout were loosely joined to the braincase and to each other, in a manner which would allow significant dorsoventral and anteroposterior motion and probably some degree of rotational freedom as well.

Cheek

The cheek is composed of lacrimal, maxilla, postfrontal, jugal, and quadratojugal, plus the squamosal complex.

The maxilla, bearing about six large, ankylosed teeth, is not suturally attached to any other bone, but is suspended from the frontal by the lacrimal anteriorly and the jugal and quadratojugal posteriorly.

The lacrimal forms the entire anterior rim of the orbit, fitting against the lateral edge of the frontal. The anterior edge of the lacrimal is thin, and the ventral edge is thickened as if it formed an articular facet for the dorsal edge of the anterior end of the maxilla. It is plausible that there was a structural association internally between the lacrimal, the maxilla, and the anterior palatal elements, but the nature of this association is not known. There is no visible structural element in the frontal-lacrimal junction that would prevent anterior-posterior sliding motion and lateral rotation of the lacrimal. The postfrontal is fitted against the postorbital process in a manner that would allow great lateral flexibility. The ventral portion of the lateral face of the postfrontal is flattened into a facet, which lies mesial to the dorsal process of the jugal (Fig. 3).

The dorsal process of the jugal bears a flange along its posterior edge, which projects mesially posterior to the shank of the postfrontal. Anteroventrally, the jugal is in contact with the dorsal edge of the

maxilla, whereas the posteroventral edge lies upon an anterior extension of the quadratojugal. The posteroventral corner of the jugal is in contact with the anteroventral element of the squamosal complex. The quadratojugal is held between the posteroventral edge of the jugal and the posterodorsal edge of the maxilla anteriorly, and forms a straight, smooth ventral edge of the cheek posteriorly. The dorsal edge rises to a thin, rounded prominence, then descends posteriorly to produce a thin point at the posteroventral corner of the cheek.

The jugal-quadratojugal-maxilla complex apparently moved as a unit, although there were no tight sutures. The jugal was capable of a posterodorsal and anteroventral sliding motion upon the postfrontal (Fig. 7A, B).

The squamosal complex (Fig. 2) is hinged to the posterolateral corner of the braincase dorsally, to the lateral edge of the quadrate ventrally, and abuts against the posterodorsal edge of the jugal anteroventrally. The ascending process can be seen to bear an anteromesially directed edge, possibly for muscle attachment, in AMNH 6966. The sinusoidal joint between the squamosal and the postorbital would allow vertical flexion, whereas maintaining contact between the anteroventral process and the jugal, a necessity if, as assumed, the posterodorsal corner of the squamosal served as a hinge during palatal protraction (Fig. 7C, D). The tympanic bones probably anchor the tympanum, and further, were not firmly attached to the underlying squamosal, a situation suggested by CM 23,056. The tympanum would thus not be affected by normal jaw motion.

Braincase

The braincase and skull roof of *Phlegethontia* are sutured into a single unit with no readily discernible internal mobility from the anterior border of the frontal to the occiput, although a limited degree of flexibility is possible at the frontoparietal joint. The small, thick nasals fit between the prongs of the frontals, dorsal to the proximal ends of the premaxillae, in movable contact with the braincase. Preorbital and postorbital processes are equally gently rounded laterally, but lightly grooved where lacrimal and postfrontal fit. Posterior to the postorbital process there is a deeply excavated temporal fossa. The fossa is separated from its counterpart in the midline by a thin sagittal crest, and prominent occipital crests form the rear border. The floor of the fossa slopes downward and outward from the sagittal crest to about mid-height of the skull, at the level of the horizontal semicircular canal. The dorsal edge of the pterygoquadrate lies ventral and lateral to this ridge. Prominent basiptyergoid processes, the *tubera basisphenoidales*, are located ventrolaterally (Fig. 4) in *P. linearis* and face anteroventrolaterally.

Pterygoquadrate

The head of the hatchet-shaped pterygoquadrate lies anterolateral to the otic expansion of the braincase (Fig. 1, 7B, C) at an angle of about 35° to the long axis of the skull. The quadrate condyle, at the posteroventral corner of the bone, is a simple hemicylinder with a posterolaterally flared end, oriented at the same angle as the dorsal edge. There is no evidence of an articular facet on the braincase of *Phlegethontia* for reception of the epipterygoid; preservation of Linton material has not favored lateral views of relatively uncrushed braincases. *Aornerpeton* has no braincase-epipterygoid articulation, whereas the braincase of *Sillerpeton* has both dorsal and lateral facets (McGinnis, 1967: Fig. 5). Palatobasal articulations of *P. linearis* and *Sillerpeton* show the possibility of anterodorsal-posteroventral sliding of the palate in relation to the braincase.

The anterior ramus of the pterygoquadrate projects forward at an angle of about 142° from the ventral third of the anterolateral edge of the posterior part. It is a strap-like, toothless bone, flaring slightly in the horizontal plane suborbitally. The anterior ramus appears to end at the anterior margin of the orbit in a ridge abutting against the palatine. In summary, the hatchet-shaped pterygoquadrate can slide anterodorsally on the basal process and abuts against the posterior end of the palatine in a movable joint.

Anterior Palatal Elements

The anterior part of the palate is best displayed in the type specimen, AMNH 6966 (Fig. 5), as a toothless strut extending from the level of the preorbital process to the region of the posteroventral end of the premaxilla. An anterior palatal element of CM 23,053 seems to bear a short lateral process or ridge which may approach the anteromesial surface of the maxilla, but additional details of the front of the palate cannot be determined.

Mandible

Two elements comprise the mandible, the dentary laterally and the postdentary mesially. The postdentary lies internal to the dentary from the symphysis back, almost totally overlapping it. There do not appear to be any sutures uniting the two elements, and as the elements are usually rotated with respect to each other in the fossils, the connection must have been predominantly ligamentous in nature. Symphyseal contact between mandibles was by small flat surfaces and there was no fusion in the midline. The articular fossa, oriented perpendicular to the long axis of the mandible, consists of a forward face, slightly convex posterodorsally, and a ventral face which is slightly convex upward.

This unusual shape is said to be more prominent in larger individuals (McGinnis, 1967). The quadrate-mandibular joint is quite smooth, and was evidently not finished in cartilage. Articulation between quadrate and mandible must therefore have been loose, the mandible capable of considerable rotation about its long axis with respect to the quadrate, as well as lateral rotation. The articular process of *P. linearis* is somewhat longer than the length of the quadrate condyle, presumably serving for insertion of a *depressor mandibularis* muscle. There are also separate, S-shaped "hyoid" bones posterior to the skull of *Phlegethontia*, a possible indicator of strong hypoglossal musculature.

Cranial Kinesis

Although details of the palatal osteology of *Phlegethontia linearis* remain obscure, enough information is now available to permit a reasonably accurate assessment of its cranial mechanics. Four principal functional units of the skull—snout, braincase, pterygoquadrate, and palatine—form a four-bar kinematic chain. The solidly ossified braincase is the fixed bar, as is typical for other kinetic skulls (Gans, 1961). The pterygoquadrate and palatine are struts for transfer of motion, and the snout, which bears lateral teeth, serves as the focus of the effort. The cheek with four functional units—the lacrimal, maxilla, postfrontal, and the orbital segment of the braincase—forms a dependent four-bar chain suspended lateral to, but sharing a portion of, the fixed bar of the principal chain. The dependent chain is tied, apparently closely, to the principal chain at the maxillo-premaxilla contact, possibly to the palatine, and probably by connective tissue associated with part of the *adductor mandibularis* complex to the pterygoquadrate. An ectopterygoid, if present, must have been attached loosely to the maxilla and pterygoquadrate. The posterior end of the maxilla was probably also ligamentously tied to the mandible. Motion of the maxilla, the other tooth-bearing bone of the upper jaw, while derived from motion of the principal chain, would be different from motion of the principal chain as a result of the suspension of the cheek. Protraction of the pterygoquadrate would result in anterolateral motion delivered to the palatines, and consequently an upward rotation of the snout about the dorsal hinge (Fig. 7). Retraction of the pterygoquadrate would depress the snout. Based upon scale models, a rotation of 8° of the pterygoquadrate could result in a rotation of the snout on the order of 30°.

Protraction of the pterygoquadrate (Fig. 7A, B) would result in an anterior rotation of the maxilla about its articulation with the lacrimal, ventral sliding of the jugal on the postfrontal joint, and potential laterodorsal rotation of the cheek on its braincase hinges. The cheek is

reinforced by the postorbital osteoderms and the squamosal-postorbital-quadratojugal complex. The osteoderms are oriented along lines from the postorbital process to the orbital edge of the maxilla as would be heterotopic ossifications in tendons. Rotation of the squamosal complex would occur with opening of the mouth, as in Fig. 7. Retraction of the pterygoquadrate would draw the maxilla and cheek posteromesially and dorsally.

Several features stiffen or otherwise limit free motion. The nasals, braced but not sutured in the notches at the anterior end of the frontal, provide a flexible limit to dorsal displacement of the premaxillae. The suspension of the cheek from the posterodorsolateral edges of the preorbital processes indicates a limited anterior rotation around these points and a large lateral component to the motion. The condition of the cheek-braincase suspension is similar to that described in the upper Cretaceous *Dinilysia* (Frazetta, 1970). In both animals elastic connective tissue at the nasal hinge and the cheek-braincase pivots would allow some motion, yet aid in return of the joints to a resting state.

Unilateral Jaw Motion

The long, slender mandible has several remarkable features. The shape and orientation of the glenoid fossa with respect to the quadrate condyle indicates an exceedingly flexible articulation. The quadratomandibular joint is capable of sustaining considerable rotation around the long axis of the mandible, and, equally importantly, lateral deflection of the mandible about the joint in excess of 60°. A large vertical swing is also probable. The apparent relatively loose connection of the dentary and postdentary might also allow some rotation of the tooth-bearing portion of the jaw about the long axis, possibly to relieve stress in the long, thin element. The mandibles were neither fused nor sutured at the symphysis and were probably bound elastically.

All details of the lower jaws indicate that they were articulated to allow great freedom of unilateral motion. The snout is also composed of clearly independent premaxillae with no tight contact in the midline, and capable of rotation about their long axes as well as lateral displacement. The cheek suspension and the nature of pterygoquadrate articulation also indicate anterolateral-posteromesial motion of the upper jaws. Frazetta (1970) has emphasized the importance of longitudinal rotation and lateral displacement of the snout elements to an effective system of unilateral feeding motions. It seems virtually certain that the feeding mechanism of *Phlegethontia* was capable of, and adapted for, unilateral motion of mandibles and upper jaws, and not for an inertial feeding system with simple cranial kinesis for increased me-

chanical advantage. The unilateral system is best known in snakes, as an adaptation for swallowing oversized prey (Gans, 1961), and is unknown in modern amphibians.

Several additional observations reinforce the unilateral feeding hypothesis. The teeth, which increase in size from the front of the premaxilla back to the end of the maxilla, are recurved and slightly compressed, for piercing and holding, and like those of the snakes are best disengaged by a forward sliding motion (Gans, 1961). The well ossified braincase coupled with the shift of the kinetic joint in the skull from the frontoparietal suture typical of crossopterygians (Thomson, 1967; Panchen, 1964) to the premaxilla-braincase zone (Frazetta, 1962, 1966, 1970) and the addition of a dependent chain, indicates an increase in complexity of kinesis with a decreased emphasis on the vertical force of the bite delivered by the jaws. The snout is essentially unbraced vertically, the maxilla is hung from the braincase without vertical bracing and the mandibles show great freedom of motion about the quadrate. None of the biting units are built for sustaining vertical stresses, all are built for sustaining longitudinal and transverse motion.

Development of a large temporal fossa indicates a strongly differentiated set of mandibular adductor muscles, probably at a complex level of neuromuscular control, and probably also associated with strong hypoglossal muscular action. The flexibility of the quadratomandibular articulation, cheek, and muzzle, and the mobility of the palate indicate a distensible gape of the mouth. The posteroventral movement of the palate during unilateral jaw closing would force prey objects ventrally and into the oesophagus, aided by the ratchet action of the teeth. In this connection it is tempting to speculate that the reduction in gastralia from a condition like that in *Ophiderpeton* to thin, widely spaced bones barely discernable in the fossils would facilitate ventral distention of the body during swallowing of large prey items. The snakes, with streptostylic quadrates and limited quadratomandibular freedom, have lateral distention of the gape as well and, with the freeing of the supratemporal at the crotaloid level, distention far in excess of that possible in *Phlegethontia*.

Muscular Anatomy

Comparison with the cranial anatomy of *Paleoherpeton* (Panchen, 1964) suggests a tentative reconstruction of the jaw musculature of *Phlegethontia*. Differentiation of the *adductor mandibularis* into three muscles, *m. pterygoideus*, *m. adductor mandibularis internus*, and *m. adductor mandibularis externus*, is entirely plausible. Posteromesial to the quadrate of *Sillierpeton* is a prominent muscle scar (McGinnis, 1967: Fig. 5) which may have served as the origin of *M. adductor arcus palatini*. *M. levator arcus palatini* probably originated on the posterior

edge of the postorbital process and adjacent temporal fossa. The separate S-shaped "hyoids" probably were the origin of the hypoglossal muscle.

The *adductor mandibularis externus* of *Phlegethontia* would originate from the temporal fossa, particularly from the sagittal and occipital crests, and insert on the dorsal and lateral surfaces of the postdentary *M. add. mand. internus* would originate on the lateral face of the pterygoquadrate and insert on the coronoid process and posteromesial surface of the postdentary. *M. pterygoideus* would originate on the pterygoid and insert on the mesial surface of the postdentary, *M. levator arcus palatini* and *adductor arcus palatini* would both insert on the anteromesial surface of the postdentary, and therefore far from the articulation or fulcrum of the mandible. The mechanical effects of a *depressor mandibularis* muscle, if present, would be negligible by contrast to that of the hypoglossal musculature.

Opening of the mouth by means of the hypoglossal muscles could be resolved into forces about the jaw joint as illustrated in Fig. 7D. These forces would tend not to move the pterygoquadrate until mandibular opening exceeded a critical angle of about 30°. Once this angle is exceeded, any further force tending to widen the angle of the gape would result in an anterior component of force applied to the pterygoquadrate, which would result in elevation of the premaxilla and a forward shift of the cheek. Closing the mouth would reverse the process, aided by the adductor musculature, including *m. pterygoideus*.

The double faceted glenoid fossa of the mandible plays a critical role in mouth opening and cranial kinesis. The normal or ventral surface of the fossa would be the principal pressure bearing surface during initial opening of the jaws or ingestion of small prey items. As jaw opening passed the 30° angle, the vertical component of force at the jaw joint would be borne by the anterior face, and the horizontal component of force would be transferred through the ventral face, bringing the kinetic mechanism fully into play.

Feeding Mechanism of Aornerpeton

The feeding mechanism of *Aornerpeton* is distinctive from that of *Phlegethontia*, as indicated by the bracing of the palate, proportional differences in the areas of origin of palatal musculature and the shape of the lacrimal. The snout is flexibly attached to the braincase, and the maxilla is capable of rotation around the lacrimal joint aided by ventral sliding of the postfrontal-jugal joint. Palatal sliding is seemingly limited by the two palatobasal articulations, anteroposterior motion of the lacrimal is precluded by its mesial lamina, and unilateral jaw action is virtually ruled out by the profile of the dentition. Understanding of relationships between the snout and the maxilla and palate awaits the

Table 1.—Comparison of the braincases of three genera of *phlegethontiids*.

<i>Phlegethontia</i>	<i>Aornerpeton</i>	<i>Sillerpeton</i>
Braincase of several bones	solid unit braincase	solid unit braincase
short cultriform process	long cultriform process	no projecting cultriform
single prootic foramen	prootic and lateral foramina	single prootic foramen
broad ventral <i>tubera basisph.</i>	broad ventral <i>tubera</i>	narrow vertical <i>tubera</i>
no "paroccipital" process	a "paroccipital" process	incipient paroccipital process
no dorsal epipterygoid articulation	no dorsal epipt. artic.	dorsal epipterygoid articulation
sagittal crest	no sagittal crest	no sagittal crest
small fenestra ovalis	large fenestra ovalis	large fenestra ovalis
narrow pterygoid	flared pterygoid	

preparation of additional specimens of *Aornerpeton*. *Aornerpeton* probably was a kinetic inertial feeder with mobile maxillae and a flexibly attached snout.

It is conceivable that *Aornerpeton* rooted in soft mud or leaf litter for food, approaching a burrowing habit. There are, however, no sutural specializations or structural braces, as seen in the skulls of amphisbaenids (Zangerl, 1944) for a strictly burrowing mode of life.

DISCUSSION

Generic Relationships

Phlegethontia linearis occurs in the late Westphalian D of Ohio (and Bohemia), *Aornerpeton mazonense* in the early Westphalian D of Illinois, and *Sillerpeton* in the Autunian (Wolfcampian) of Oklahoma. Morphologic relationships between the three are not related to time of occurrence, and signify a longstanding and broad-scale adaptive diversification. Comparison of the braincases of the three reveals the depth of this diversity (Table 1).

Aornerpeton, the oldest, and *Sillerpeton*, the youngest, share the advanced fusion of braincase, the lack of a sagittal crest, and the large fenestra ovalis, all presumably derived from a *Phlegethontia*-like condition, although size of the fenestra ovalis may be inversely related either to the size or to the age of the animal. Additionally, the structure McGinnis (1967: Fig. 5a, c) calls a "muscle scar" in *Sillerpeton* may be an incipient "paroccipital" process, as in *Aornerpeton*. There is little difference between *Phlegethontia* and *Sillerpeton* in size of cultriform process, which may be plesiomorphic, and in the prootic foramen, which may be derived (Panchen, 1964). *Phlegethontia* and *Aor-*

nerpeton have similar *tubera basisphenoidales*, and similarly lack a dorsal shelf for epipterygoid articulation.

Clearly, although the three are related, they are divergent. The palate of *Sillerpeton* may have been capable of considerable rotation about the dorsal articulation, which, guided by the *tubera*, would have translated into anteroposterior swing. This must remain speculative until more of this animal is found, but palatal articulation, and therefore the nature of the feeding mechanism, is not derivable from either the *Aornerpeton* or *Phlegethontia* conditions. Thus, although only the braincase of *Sillerpeton* is known at present, it is sufficiently distinctive to warrant generic separation.

Habitat

Many anatomical features of the Phlegethontiidae argue for primarily terrestrial adaptations. The large tympanum and narrow-shafted stapes are indicators of terrestrial sound reception. There are no traces of branchial or hyoid elements which might have supported an oropharyngeal pump or gills. The "hyoids" are not connected in the ventral midline, lie posterior to the skull, and could have acted only as origin and insertion for hypoglossal and trunk musculature. There is no indication of a larval, or less ossified stage of development. The vertebrae, with stout transverse processes, have very low spines, unlike vertebrae in amphibians which swim by lateral undulation, such as the urocordylid nectrideans (Baird, 1965). Phlegethontiids, like many snakes, may have entered the water to feed, but were primarily terrestrially adapted.

Relationships with other Families

The Ophiderpetontidae share a number of unique derived postcranial characters with phlegethontiids. These are the large number of trunk vertebrae, over 100 (Baird, 1964), and the form of these vertebrae, the total lack of limbs and girdles, and the K-shaped ribs. *Ophiderpeton* shows extreme postorbital elongation, a very short snout, no skull roof fusions, retention of simple, primitive premaxillae, and posttemporal emargination of the skull. The palate and cheek are primitively laterally mobile, articulating with the ventral edge of the skull roof. The palate projects posteroventrally beyond the skull, and articulates with a plesiomorphous lower jaw. Cranial osteoderms cover the outside of the skull, a peculiarly apomorphic character. Characters in ophiderpetontid skull evolution are opposite in direction to those of the phlegethontiids, indicating sister groups with a basic lateral undulatory propulsive system but diverging on feeding adaptation.

Among known early Mississippian Amphibia, the postorbital elongation of the skull and large number of trunk vertebrae of the adelogyrinid

microsaurs (Carroll and Baird, 1968) are reminiscent of trends toward aïstopods. Loss of cheek and palatal mobility, and retention of weak limbs and girdles (Thomson and Bossy, 1970) indicate a sister group status at best.

The urocordylid Nectridea, currently under investigation by Bossy, are represented by several individuals with skulls in the Carnegie Museum collections from Linton, Ohio. These specimens, which are close to *Ptyonius*, show lateral cheek and palatal mobility, a postfrontal-jugal joint, and a supratemporal which lay loosely over a secondary sutural connection between parietal and tabular. The fossa formed in this manner is analogous to the temporal fossa of *Phlegethontia*. Cranial kinesis is present in *Ptyonius* centering around a frontoparietal joint and seeming to involve the entire snout, cheek, and palate rotating about the otico-occipital portion of the skull (Thomson and Bossy, 1970).

As Thomson and Bossy (1970) have indicated, particular sets of skull bone arrangements have specific functional determinants. Similarities between *Ptyonius* and *Phlegethontia* in skull bone arrangement involve patterns adapted from common ancestors with cranial kinesis, perhaps ancestors little modified from the crossopterygian kinetic mechanism, and these patterns have evolved along pathways dictated by functional necessities such as the development of a temporal fossa for expanded palatal musculature. Similarities between these two genera are put into perspective by the differences between *Sauroplorea*, *Urocordylus* (Thomson and Bossy, 1970), and *Ptyonius* among the urocordylids, (Baird, 1965). The urocordylid Nectridea differ still further from the derived keraterpetontid Nectridea, a group with totally akinetic skulls, lacking a separate supratemporal element. All Nectridea do share a basically similar cranial osteology, similar vertebrae, elongation and compression of the tail, and a secondarily permanent aquatic habitat. Characters shared between Nectridea and Aïstopoda seem either to be plesiomorphous, or to be shared on the broadest subdivision of the Paleozoic Amphibia.

The Anthracosauria retain lateral cheek and palatal mobility and potential for cranial kinesis (Thomson and Bossy, 1970). Further, differentiation of neck and trunk vertebrae and the pattern of centrum formation are close to that of *Phlegethontia*. The anthracosaurs seem to retain features of a feeding mechanism in common with the aïstopods and with more generalized nectrideans.

Comparison with Snakes

The functional morphology of snake skulls has been analyzed in detail by Frazetta (1962, 1966, 1970) and Gans (1961, 1973). The jaws of snakes differ in many respects from those of *Phlegethontia*, but par-

ticularly in the reduction of the premaxillae, teeth on the palatines, the loose suspension of the quadrate from the rear of the skull, the tight quadratomandibular articulation, and the dentary-surangular joint. The snakes can be roughly divided into three major levels of organization, boid, colubroid and crotaloid (Frazetta, 1970; Gans, 1961), on the basis of increased freedom of motion of the maxilla and supratemporal. *Phlegethontia* can be compared to the boid level of organization, somewhat advanced over the relatively stiff suspension of the cheek and snout in the upper Cretaceous snake *Dinilysia* (Frazetta, 1970). The active role played by the *pterygoideus*, *protractor* and *retractor pterygoidei* in the movement of both maxilla and palates of snakes (Frazetta, 1966) suggests a similar function of these muscles in *Phlegethontia*. The role of mandibular and palatal rotation in the swallowing of very large prey (Frazetta, 1970) is also analogous to the articular arrangements of *Phlegethontia* between premaxilla, cheek, and braincase, in the apparently loose articulation between the rear of the maxilla and the pterygoquadrate, and in the quadratomandibular articulation. *Phlegethontia*, although phyletically unrelated to snakes, parallels them closely in body form and cranial function.

SUMMARY

The cranial and cervical osteology of *Phlegethontia linearis* is described, and that of *Aornerpeton mazonense* (Gregory, 1948) and *Sillerpeton permianum*, new genera, are compared and contrasted with it. The three genera differ greatly in endocranial structure and in the functional anatomy of their feeding mechanisms.

The feeding mechanism of *Phlegethontia linearis* displays cranial kinesis with unilateral movement of the jaws, in a manner analogous to snakes. Four principal functional units of the skull, the snout, braincase, pterygoquadrate, and palatine, form a four-bar kinematic chain. The cheek, composed of lacrimal, maxilla, postfrontal, and jugal, is suspended from preorbital and postorbital processes of the braincase as a dependent four-bar chain and is linked to the rear of the braincase and palate by the squamosal, postorbital, and quadratojugal. The mandible serves as the lever initiating kinesis when depression exceeds a critical angle. Teeth, borne on the rim of the mouth only, are strong and recurved, and aid in unilateral feeding motions. The articular arrangements of the upper and lower jaws indicate a capacity to ingest large prey items, and although the pterygoquadrates are incapable of significant lateral dislocation, structure of the jaw joint and reduction of the gastralia may indicate that the ventral surface of the body was capable of considerable distention.

The feeding mechanism of *Aornerpeton* lacks the palatal mobility of *Phlegethontia*, possibly indicating an inertial feeding mechanism. The

upper jaw and cheek bones, however, are capable of motion analogous to those of protacanthopterygian teleosts.

Postcranial characters unite the functionally diverse Phlegethontiidae with the very differently specialized Ophiderpetontidae. Of the other lepospondylous amphibians the urocordylid Nectridea share primitive characters of the feeding mechanism, but exhibit certain postcranial trends unlike those which could have led to the aistopod propulsive system. The adelogyrinids show such trends, however, and might be a sister group. The Anthracosauria share characters of the feeding mechanism derived from the same basal condition as both Nectridea and Aistopoda, and seem to share vertebral centrum formation and differentiation of a neck in common with phlegethontiids. There is little direct evidence for deriving the aistopoda from any presently known amphibian group.

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BATS FROM SOUTHERN HAITI

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ABSTRACT

A collection of 450 specimens of bats from the Departement du Sud, Haiti, is described. Fifteen of the 17 species previously recorded from Hispaniola are represented, and *Noctilio leporinus* is reported from Haiti for the first time. Reproductive information for the months of January, May, June, August, and December is presented. *Macrotus waterhousii* is seasonally monoestrous, as on the mainland. The two species of stenodermines, *Artibeus jamaicensis* and *Phyllops haitiensis*, do not show bimodal seasonal polyestry as do stenodermines in Central America. *Monophyllus redmani* and the phyllonycterines may be seasonally monoestrous. Differences in reproductive biology between Haitian bats and closely related species on the Central American mainland may be correlated with differences in climate between the two areas.

INTRODUCTION

Studies of the systematics, biogeography, and ecology of Antillean bats are often hampered by a paucity of data. It became possible recently to collect bats intensively in the Departement du Sud, Republic of Haiti, an area hitherto poorly known mammalogically. We present the results of our collections and analyses, including mensural data for

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series of bats of some species known previously from isolated specimens, and reproductive data for some species from the months of January, May, June, August, and December.

Owing to the difficulties of working in Haiti, most past collections of bats from Hispaniola were made in the Dominican Republic. Recent work in the Republic of Haiti dates from Miller's (1918, 1929) reports on bats found as skulls on the floors of caves near Port-de-Paix and St. Michel de l'Atalaye. In 1939 Ivan T. Sanderson collected in southern Haiti using a 1923 Rolls-Royce Silver Ghost as his field vehicle (Sanderson, 1939). Sanderson's bats were discussed by Sanborn (1941) and Hershkovitz (1951). In 1955 Koopman reported on a 1929 collection of cave remains of bats from the Ile de la Gonave. To our knowledge, no extensive netting of Haitian bats was done prior to 1973.

Between 29 December 1973 and 10 January 1974, D. Klingener, C. Woods, C. Butterfield, and V. Naples collected bats in the vicinity of Paillant, on the mountainside above Miragoâne, using nets that had been set for study of migratory birds. J. W. Bickham and J. C. Patton netted bats near Paillant and in the ravines above and below that town between 13 and 28 August 1974. Between 17 December 1974 and 12 January 1975, D. Klingener, C. Woods, and C. Butterfield obtained bats near Paillant and traveled out along the road to Anse-a-Veau, where bats were collected at Charlier. In May and June 1975, C. Woods and a field party from the University of Vermont collected bats at the western tip of the southern peninsula, including some from nets set on the slopes of the Pic de Macaya.

The island of Hispaniola is divided into two highland areas (the "North Island" and the "South Island," likely separated by a seaway in the past) by the Plaine du Cul de Sac, which isolates the southern peninsula of Haiti and the Barahona Peninsula of the Dominican Republic from the highlands of northern Haiti and the Dominican Republic (Williams, 1961). The southern peninsula of Haiti has two highland regions, the eastern Massif de la Selle (maximum elevation, 2,674 m) and the western Massif de la Hotte (maximum elevation being the Pic de Macaya, 2,347 m). The lowland isthmus between the two massifs is the Trouin Valley between Jacmel and Grand Goâve (Schwartz, 1973). Our collections were made at localities ranging from sea level to the slopes of the Pic de Macaya in the Massif de la Hotte, from Miragoâne westward to Anse d'Hainault.

Haiti is a mountainous country with few streams or playas. Caves in the limestone are abundant, but these are small and difficult for humans to enter. Depending on location, rainfall varies between 524 and 2,124 mm per year. There are two rainy seasons, one in the spring, the other in the autumn (Woodring et al., 1924). The evergreen tropical rainforest described by Columbus in 1493 is mostly gone owing to lumbering,

agriculture, and the burning of wood for charcoal. In the southern peninsula, forest persists only in deep ravines and on steep mountainsides in the extreme west (C. Woods, personal communication). Elsewhere the uncultivated parts of mountains are covered by dry thorn scrub, with somewhat thicker vegetation persisting in ravines and dry washes. The human population and its domestic animals continue to increase in density, and further deforestation will probably occur.

METHODS AND MATERIALS

Our specimens were taken primarily by netting and were preserved as skin/skull, skin/skeleton, skeleton only, or fluid preparations. The specimens are deposited in The American Museum of Natural History (AMNH), The Museum, Texas Tech University (TTU), and the Museum of Zoology, University of Massachusetts (UMA). We collected a total of 450 specimens, referable to 15 species. Two species, *Tadarida macrotis* and *Natalus major*, previously recorded from the island (Varona, 1974), are not represented in our collection. Some Cuban specimens of *Phyllonycteris poeyi* in the collection of the National Museum of Natural History were also used for comparative purposes. Measurements of forearm and cranial distances are standard ones and were taken by one of us (HHG) with dial calipers accurate to 0.1 mm. In the Tables (1 through 4), measurements of individual specimens are listed for series of four or fewer. For larger series, the mean, observed range, and standard deviation are indicated.

A few field weights were taken by one of us (DK) with a Pesola scale. Reproductive conditions were determined by gross dissection of skin/skeleton and skin/skull specimens in the field and by later dissections of fluid preserved animals. Sizes of embryos are given as crown-rump lengths. Reproductive data from some specimens in the University of Vermont collection are included and were taken by C. Woods. Those animals are not included in our list of specimens examined. In all cases pregnant bats were carrying single young. We observed no instances of twinning.

Varona (1974) provided a valuable summary of distribution of bats among the Greater and Lesser Antillean islands. His taxonomic treatment is in many cases unorthodox. As he has not given reasons for his taxonomic usage, we have chosen not to follow him in many instances. We did not compare our bats with series from northern Haiti or from the Dominican Republic. Buden (1975b) found no difference between series of *Macrotus waterhousii* from the North and South islands. Similar comparisons have not been made for other species.

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Charles Woods, University of Vermont, provided the impetus for work on the island, assisted in the field work, and contributed reproductive data on bats collected by him and by his students. Field work was also done by Carl Butterfield, John Bickham, John Patton, and Virginia Naples. To all of these individuals we are grateful.

Charles O. Handley, Jr., and Karl F. Koopman permitted examination of specimens in their care, and Dr. Koopman unstintingly shared his insights into the systematics and evolution of Antillean bats. A number of colleagues read an earlier draft of this manuscript. We thank them for suggesting improvements.

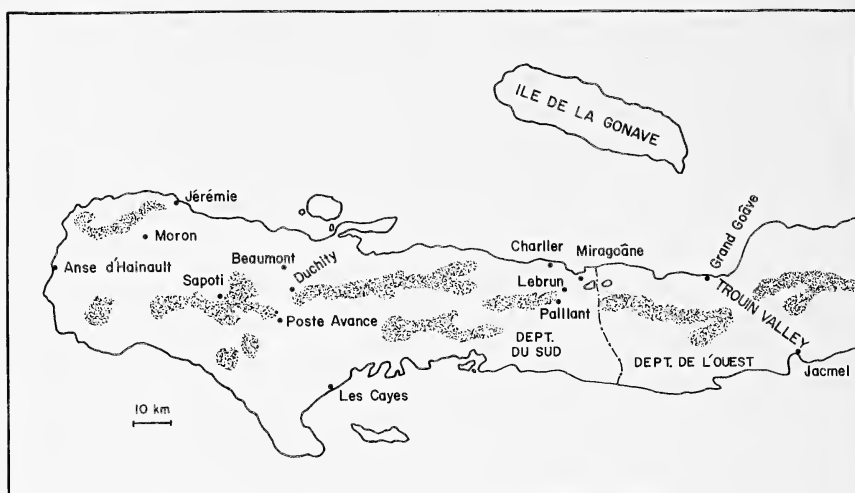


Fig. 1.—Map of the southern peninsula of Haiti showing localities mentioned in the text. The highest mountain peaks and ridges are shaded.

Field work was assisted by grants from the National Geographic Society (to C. Woods), from the University of Massachusetts Faculty Research Grant Program (to D. Klingener), and by National Science Foundation grant GB-41105 to R. J. Baker and H. H. Genoways.

LOCALITIES

Most of the bats were collected in the vicinity of Miragoâne (Fig. 1). Paillant is 8 km SW Miragoâne, 1 km S, 1 km E Lebrun at an elevation of 580 m. Paillant is the site of the Reynolds Haitian Mines residential compound. Surrounding habitat is dry thorn scrub, but thicker vegetation persists in ravines and draws. Nets were also set in ravines some distance from Paillant. Locations of these are given with reference to Lebrun, a town bypassed by the road between the Reynolds bauxite mine and the loading dock, 1 km W Miragoâne.

Charlier is a town 10 km W Miragoâne and is at sea level. The Rivière Charlier breaks up into stagnant pools before emptying here into the Caribbean. Nets were set along the stream as it passes through a banana plantation and over pools near the ocean.

Most of the bats from the extreme western part of the southern peninsula came from two localities (Fig. 1). Duchity (spelled Dichity on some maps) is 6 km S Beaumont on the road between Beaumont and Poste Avance. It is on the Rivière Glace and is 732 m above sea level. The area is planted in coffee, but forest persists in the deeper ravines. Sapoti (also spelled Zapoti) is 19 km SW Beaumont at 1,211 m on the

Table 1.—Measurements of *noctilionid* and *mormoopid* bats from southern Haiti.

Number and sex	Forearm	Greatest length of skull	Condylobasal length	Zygomatic breadth	Postorbital constriction	Breadth of braincase	Length of maxillary toothrow	Breadth across upper molars
<i>Noctilio leporinus</i>								
AMNH 236,651 ♂	88.0	29.6	25.3	20.5	7.2	13.8	10.5	13.2
AMNH 236,652 ♂	85.6	29.0	25.1	20.3	7.4	14.0	10.6	12.8
AMNH 236,653 ♀	86.1	26.3	23.7	19.0	7.2	13.7	10.2	12.2
<i>Pteronotus fuliginosus</i>								
AMNH 236,654 ♀	37.7	14.7	13.2	7.7	2.9	6.6	5.7	5.3
<i>Pteronotus parnellii</i>								
TTU 22,508 ♂	50.6	19.0	17.3	10.3	3.7	9.2	7.9	6.8
TTU 22,501 ♂	49.7	19.0	17.4	10.3	3.7	9.1	7.9	6.7
TTU 22,502 ♂	50.0	19.4	17.5	10.6	3.9	9.6	8.0	6.9
TTU 22,507 ♂	50.6	19.3	17.8	10.8	3.7	9.2	8.0	6.9
TTU 22,504 ♀	51.4	19.0	17.4	10.5	3.8	9.1	7.9	7.0
TTU 22,509 ♀	50.0	19.0	17.2	10.4	3.6	9.5	8.1	6.8
TTU 22,510 ♀	52.9	19.3	17.6	10.6	3.7	8.9	6.0	6.8
TTU 22,511 ♀	50.3	18.9	17.0	10.3	3.6	9.1	8.0	6.8
<i>Mormoops blainvillii</i>								
TTU 22,497 ♂	46.1	13.8	13.6	8.6	4.3	7.3	7.6	6.1
TTU 22,490 ♂	45.5	14.2	13.9	8.5	4.1	7.5	7.4	6.2
TTU 22,491 ♂	47.2	14.1	13.7	8.3	4.2	7.3	7.3	6.1
TTU 22,493 ♂	46.9	14.3	14.0	8.1	4.2	7.3	7.5	6.1
TTU 22,496 ♀	47.1	13.6	13.5	8.2	4.2	7.2	7.5	5.9
TTU 22,492 ♀	47.1	14.0	13.7	8.1	4.2	7.3	7.4	5.8
TTU 22,494 ♀	48.4	14.5	14.2	8.4	4.3	7.5	7.4	5.7

north slope of the Pic de Macaya. The mountain above the settlement is forested.

ACCOUNTS OF SPECIES

Family Noctilionidae

Noctilio leporinus mastivus (Vahl)

Specimens examined (4).—Charlier, 2 (1 AMNH, 1 UMA); 1 km W Miragoâne, 2 (AMNH).

Measurements of three of our specimens are listed in Table 1. They agree with measurements given for *N. l. mastivus* by Davis (1973). One male weighed 78 g; a female weighed 60 g.

The only previous records of this species from Hispaniola are from the Dominican Republic (Armstrong and Johnson, 1969). Our bats represent the first records from the Republic of Haiti.

The two bats from Charlier were netted at dusk over a shallow stagnant pool in which small fish were active. The specimens from 1 km W Miragoâne were shot as they fished over the Caribbean in a lagoon used as a loading area for bauxite ships by Reynolds Haitian Mines. Bats were observed on several nights at this location, flying regular patterns, passing repeatedly over and touching water at places where schools of small fish clustered. Bats were not there on windy evenings when the water was not smooth. Attempts to net the bats over the Caribbean were unsuccessful.

The female taken on 10 January was not pregnant. Two males taken on 21 December and 10 January had scrotal testes measuring 6 mm. A male taken on 21 December had partially scrotal testes which measured 7 mm.

Family Mormoopidae

Pteronotus fuliginosus fuliginosus (Gray)

Specimen examined (1).—Sapoti, 1 (AMNH).

Measurements of our single specimen are given in Table 1. It is a female taken on 27 May while carrying a single 14 mm embryo.

Pteronotus parnellii pusillus (G. M. Allen)

Specimens examined (13).—Paillant, 8 (TTU); 4 km S Lebrun, 4 (TTU); Sapoti, 1 (AMNH).

Measurements of seven specimens are listed in Table 1. In general, measurements of our specimens agree with those given for other Hispaniolan examples by Smith (1972: 110).

A female netted on 27 May was not pregnant; five females collected between 19 and 23 August also showed no sign of reproductive activity.

Table 2.—Measurements of *phyllostomatine*, *glossophagine*, and *stenodermine* bats from southern Haiti.

Number and sex	Forearm	Greatest length of skull	Condylabasal length	Zygomatic breadth	Postorbital constriction	Breadth of braincase	Length of maxillary toothrow	Breadth across upper molars
<i>Macrotus waterhousii</i>								
TTU 22513 ♂	53.2	26.7	22.7	12.9	4.4	9.6	9.8	8.3
TTU 22522 ♂	52.5	25.9	—	12.3	4.3	10.0	10.0	8.2
9 ♀♀	54.4 (53.3–55.5) ±0.70	25.9 (25.0–26.4) ±0.45	22.0 (21.5–22.6) ±0.32	12.4 (11.8–12.9) ±0.32	4.2 (4.0–4.4) ±0.11	9.6 (9.2–10.1) ±0.28	9.9 (9.6–10.2) ±0.20	7.9 (7.7–8.2) ±0.16
<i>Monophyllus redmani</i>								
9 ♂♂	40.5 (39.5–41.4) ±0.71	21.7 (21.2–22.3) ±0.34	20.2 (19.9–20.7) ±0.27	9.3 (9.1–9.5) ±0.14	4.1 (3.9–4.3) ±0.13	9.0 (8.7–9.4) ±0.21	7.8 (7.6–7.9) ±0.10	5.0 (4.8–5.1) ±0.11
10 ♀♀	39.4 (38.6–40.8) ±0.64	21.7 (21.3–22.0) ±0.20	20.2 (19.8–20.7) ±0.05	9.1 (8.8–9.3) ±0.11	4.2 (4.1–4.3) ±0.24	9.0 (8.7–9.3) ±0.22	7.8 (7.6–8.0) ±0.13	4.9 (4.6–5.2) ±0.19
<i>Artibeus jamaicensis</i>								
16 ♂♂	57.3 (55.0–59.0) ±1.38	27.4 (26.5–28.2) ±0.48	24.4 (23.2–25.2) ±0.54	16.6 (15.8–17.3) ±0.50	7.0 (6.5–7.4) ±0.24	11.9 (11.6–12.3) ±0.20	9.6 (9.0–10.2) ±0.26	12.1 (11.2–12.6) ±0.36
24 ♀♀	57.7 (54.5–60.9) ±1.73	27.5 (26.8–28.3) ±0.41	24.3 (23.6–25.4) ±0.37	16.5 (16.0–17.3) ±0.31	6.9 (6.5–7.0) ±0.24	11.9 (11.5–12.8) ±0.29	9.5 (9.0–10.1) ±0.24	12.1 (11.4–12.8) ±0.31
<i>Phyllops haitiensis</i>								
17 ♂♂	40.6 (38.6–42.1) ±1.11	19.7 (19.0–20.2) ±0.31	17.5 (16.8–17.8) ±0.24	13.1 (12.5–13.6) ±0.30	5.4 (5.2–5.7) ±0.14	9.8 (9.6–10.1) ±0.15	5.7 (5.5–5.9) ±0.11	7.9 (7.8–8.2) ±0.15
25 ♀♀	42.6 (40.5–44.8) ±1.08	20.3 (19.6–20.7) ±0.26	18.1 (17.3–18.5) ±0.26	13.4 (12.6–13.8) ±0.27	5.5 (5.3–5.7) ±0.15	10.0 (9.5–10.3) ±0.19	6.0 (5.7–6.2) ±0.13	8.2 (7.5–8.5) ±0.22

Testes in three males netted on 19 August were small, measuring 2 mm or less.

Family Phyllostomatidae

Macrotus waterhousii waterhousii Gray

Specimens examined (22).—Paillant, 5 (4 TTU, 1 UMA); 2 km N, 2 km E Lebrun, 9 (TTU); 1 km S Lebrun, 1 (TTU); 4 km S Lebrun, 5 (TTU); 2 km SE Duchity, 2 (AMNH).

Greenbaum and Baker (1976) discussed the relationships among mainland and Antillean populations of this species, including the population of southern Haiti. According to Anderson and Nelson (1965) and Buden (1975*b*) the name for this population is *M. w. waterhousii*, which was described from Haiti. Measurements of our bats are listed in Table 2. One female weighed 19.5 g.

One female netted on 7 January was not pregnant. Of six adult females taken on 16 May, five were pregnant. The largest embryo measured 34 mm. None of the 14 females taken between 19 and 27 August was pregnant. Testes of the single male netted on 23 August were 2 mm long.

Monophyllus redmani clineadaphus Miller

Specimens examined (72).—Paillant, 40 (13 AMNH, 17 UMA, 10 TTU); 2 km N, 2 km E Lebrun, 2 (TTU); 1 km E Lebrun, 26 (TTU); 1 km S Lebrun, 3 (TTU); 8 km N Beaumont, 1 (TTU).

We follow Schwartz and Jones (1967) and Buden (1975*a*) in their taxonomic treatment of the *Monophyllus* of Hispaniola. Measurements of our specimens are in Table 2. Weight of 21 individuals averaged 10.9 g (range, 8–13).

Monophyllus is one of the more commonly collected bats in Haiti. It was taken in numbers, along with *Artibeus jamaicensis*, in dry thorn scrub. It was also commonly seen with that species during the day roosting in shallow caves and excavations.

Twenty-one females were taken between 3 and 9 January, and 28 between 14 and 27 August. None were pregnant, and none showed any sign of recent parturition. Two females taken on 27 May were pregnant, the embryos measuring 15 and 18 mm. Males netted in January and August had small abdominal testes ranging in length from 1 to 3 mm.

Artibeus jamaicensis jamaicensis Leach

Specimens examined (151).—Paillant, 58 (32 UMA, 12 AMNH, 14 TTU); 2 km N, 2 km E Lebrun, 5 (TTU); 1 km E Lebrun, 53 (TTU); 1 km S Lebrun, 11 (TTU); 4 km S Lebrun, 2 (TTU); Charlier, 21 (15 UMA, 6 AMNH); 8 km N Beaumont, 1 (TTU).

Measurements of our specimens are listed in Table 2. Average weight of 19 individuals was 35.5 g (range, 32–40.5).

Presence of both upper and lower third molars varies geographically in this species. In samples from the Pacific versant of México north of Oaxaca, 99% of the individuals have M^3 present (Handley, 1966). In samples drawn from the remainder of the range of the species in Middle America, 98% show bilateral absence of this tooth (Davis, 1970). The tooth is absent in all of our Hispaniolan specimens. Elsewhere in the Antilles the M^3 is present in 100% of a sample from Trinidad, 94% of a sample from Grenada, and 12% of a sample from St. Vincent (Jones and Phillips, 1970). However, further north in the Lesser Antilles (Barbados and St. Lucia) the tooth is absent in all bats examined (Jones and Phillips, 1970). Absence of M_3 is rare in mainland Middle American populations, less than 3% of the bats studied by Davis (1970) showing loss of the tooth on one or both sides. In the specimens that have crania available for examination in our Haitian sample, in contrast, the M_3 is absent bilaterally in 21% (4 specimens), absent on one side only in 11% (2 specimens), and present bilaterally in 68% (13 specimens).

Artibeus jamaicensis is the most abundant bat in our collections, accounting for about a third of the specimens preserved. In addition to these, many more were released in the field. It is extremely common in the dry deforested regions and abundant in the vicinity of cultivated fruit. It is also the bat most commonly seen in small caves and excavations near Miragoâne. A cluster of six was seen hanging during the daytime in a shallow embrasure (less than a meter deep) in the limestone in a canyon downhill from Paillant.

Two of three females obtained on 13 June were not pregnant, whereas one had a large embryo. Of 41 females netted between 14 and 16 August, 17 were not pregnant, 20 had enlarged uteri, and four had embryos measuring 6, 8, 9, and 10 mm. Eighteen females taken between 21 December and 9 January evinced the following reproductive conditions: 12 were not pregnant; six had enlarged uteri with visible embryos (smaller than 3 mm); two had larger embryos (12 and 18 mm).

Length of testes in 10 males netted in late August averaged 7.1 mm (range, 3–10). The same measurement averaged 6.9 mm (range, 4–8) in 21 males caught in late December and early January.

Phyllops haitiensis J. A. Allen

Specimens examined (104).—Paillant, 44 (34 TTU, 7 AMNH, 3 UMA); 2 km N, 2 km E Lebrun, 9 (TTU); 1 km E Lebrun, 21 (TTU); 1 km S Lebrun, 1 (TTU); 4 km S Lebrun, 29 (TTU).

Phyllops haitiensis appears to show secondary sexual dimorphism in most dimensions of body and cranium, with the female being the larger. Similar variation is characteristic of the closely related Puerto Rican

species *Stenoderma rufum* (Jones et al., 1971). *Phyllops haitiensis* may be conspecific with *P. falcatus* of Cuba (Jones and Carter, 1976). Measurements of our specimens are listed in Table 2.

Phyllops is second in abundance only to *Artibeus jamaicensis* in our collections. It was netted more frequently, however, in thickly vegetated ravines than in drier scrub thorn habitats.

All six females taken between 4 and 9 January were pregnant; lengths of embryos ranged from 6.5 to 14 mm. Of 54 females netted between 14 and 27 August, 27 were not pregnant, eight had enlarged uteri, 14 had embryos ranging in length from 10 to 43 mm, and five had enlarged postpartum uteri. Five of eight females caught on 27 May were pregnant. Length of testes averaged 4.3 mm (range, 1–6) in 10 males netted in late August.

Brachyphylla pumila Miller

Specimens examined (6).—Paillant, 4 (TTU); 1 km E Lebrun, 1 (TTU); Charlier, 1 (UMA).

Buden (1977) viewed *B. pumila*, and all other named populations of *Brachyphylla*, as members of a single species, *B. cavernarum*. We withhold judgment on the taxonomic assignment of our Haitian material until the systematic studies of Pierre Swanepoel, now in progress, are complete. Measurements of our specimens are listed in Table 3.

Brachyphylla is apparently a rare bat in southern Haiti. In mist nets set in ravines near Paillant and alongside and across a stream near a banana plantation at Charlier, *Artibeus jamaicensis* outnumbered *Brachyphylla* approximately 50 to 1.

A female netted on 21 December and four females netted between 21 and 25 August were not pregnant, but one of the August females was lactating. A male taken on 14 August had testes 3 mm long.

Erophylla sezekorni bombifrons (Miller)

Specimens examined (5).—1 km S Lebrun, 2 (TTU); 1 km E Lebrun, 2 (TTU); 4 km S Lebrun, 1 (TTU).

Buden (1976) placed all Caribbean populations of *Erophylla* in *E. sezekorni*, but recognized the Puerto Rican and Hispaniolan bats as a distinct subspecies. Measurements of two females are listed in Table 3.

Our specimens were taken in ravines near Paillant. None of the five females netted between 16 and 21 August were pregnant.

Phyllonycteris poeyi obtusa Miller

Specimens examined (37).—Paillant, 6 (2 AMNH, 1 UMA, 3 TTU); 2 km N, 2 km E Lebrun, 1 (TTU); 1 km E Lebrun, 10 (TTU); 1 km S Lebrun, 14 (TTU); 4 km S Lebrun, 6 (TTU).

Table 3.—Measurements of phyllonycterine bats from southern Haiti.

Number and sex	Forearm	Greatest length of skull	Condylobasal length	Zygomatic breadth	Postorbital constriction	Breadth of braincase	Length of maxillary toothrow	Breadth across upper molars
<i>Brachyphylla pumila</i>								
TTU 22761 ♂	58.8	28.2	25.0	14.7	6.2	11.2	9.5	9.4
TTU 22760 ♀	58.0	28.4	25.1	15.5	6.3	11.7	9.5	10.1
TTU 22764 ♀	58.3	28.1	24.8	14.6	6.4	11.9	9.5	10.1
TTU 22762 ♀	58.8	28.1	25.3	14.9	6.3	11.7	9.4	9.9
<i>Erophylla sezekorni</i>								
TTU 22767 ♀	46.8	24.4	22.5	11.7	4.5	10.2	8.1	6.7
TTU 22768 ♀	46.5	23.4	21.1	—	4.4	9.8	7.9	6.1
<i>Phyllonycteris poeyi</i>								
7 ♂	48.4 (47.5–49.8) ±0.80	25.1 (24.5–25.7) ±0.43	22.6 (21.6–23.4) ±0.55	—	5.5 (5.3–5.7) ±0.12	10.5 (10.2–11.0) ±0.30	7.4 (7.2–7.6) ±0.14	7.1 (6.7–7.5) ±0.34
11 ♀	47.9 (42.6–49.8) ±1.13	24.2 (23.7–24.7) ±0.35	22.2 (21.6–23.1) ±0.41	—	5.5 (5.2–5.7) ±0.13	10.3 (10.0–10.9) ±0.30	7.4 (7.1–7.7) ±0.17	7.0 (6.8–7.2) ±0.13

Forearm and cranium dimensions of our specimens do not differ from those of a series of three males and three females of *P. poeyi poeyi* from Guanajay, Cuba, in the National Museum of Natural History. There are also no observable qualitative cranial differences between these populations. Measurements of our specimens are listed in Table 3. Two adult females weighed 20.0 and 21.1 g; a male weighed 20.5 g.

Our specimens were taken in ravines, though a few were found in the drier scrub on hillsides. One bat was carrying fruit when it was caught in the net.

Three females caught on 17 December were pregnant, the embryos measuring 15, 20, 22 mm. A female netted on 6 January and 22 females netted between 19 and 27 August were not pregnant. Length of testes in seven males collected between 21 and 27 August averaged 4.1 mm (range, 2–7).

Family Vespertilionidae

Eptesicus fuscus hispaniolae Miller

Specimens examined (4).—Sapoti, 4 (AMNH).

Measurements of our specimens are listed in Table 4. All were males taken on 27 May and had testes ranging from 5 to 6 mm in length.

Lasiurus borealis minor Miller

Specimen examined (1).—Paillant, 1 (TTU).

Measurements of our specimen are listed in Table 4. The animal was a non-pregnant female taken on 14 August. Hall and Kelson (1959: 191) recognized a number of distinct species of red bats, including *L. minor*, in the Antilles. Koopman et al. (1957) and Varona (1974) considered them to represent subspecies of the mainland species *L. borealis*. We follow this latter course in this paper.

Family Molossididae

Tadarida brasiliensis constanzae Shamel

Specimens examined (3).—Anse d'Hainault, 2 (AMNH); Sapoti, 1 (AMNH).

Measurements of our three specimens are listed in Table 4. The specimens from Anse d'Hainault were taken in attics. The one from Sapoti was netted.

A female taken on 27 May was pregnant. Two females taken on 10 June were also pregnant, carrying embryos measuring 15 and 20 mm. A male taken on 27 May had testes 2.5 mm long.

Table 4.—Measurements of vespertilionid and molossid bats from southern Haiti.

Number and sex	Forearm	Greatest length of skull	Condylobasal length	Zygomatic breadth	Postorbital constriction	Breadth of braincase	Length of maxillary toothrow	Breadth across upper molars
<i>Eptesicus fuscus</i>								
AMNH 236699 ♂	48.5	18.7	17.1	12.3	4.2	8.6	6.5	7.7
AMNH 236700 ♂	47.6	19.0	17.5	12.4	4.2	8.1	6.7	7.6
AMNH 236701 ♂	46.6	18.1	16.8	12.4	4.3	8.4	6.7	7.4
AMNH 236702 ♂	45.5	17.9	16.4	11.9	4.2	8.4	6.3	7.2
<i>Lasiurus borealis</i>								
TTU 22804 ♀	39.8	13.2	12.0	8.9	4.3	7.2	4.3	6.4
<i>Tadarida brasiliensis</i>								
AMNH 236705 ♂	40.0	16.0	14.7	9.2	3.6	8.5	5.5	6.6
AMNH 236703 ♀	41.7	15.7	14.6	9.2	3.6	8.5	5.5	6.4
AMNH 236704 ♀	40.2	15.9	14.5	9.1	3.8	7.9	5.7	6.5
<i>Molossus molossus</i>								
7 ♂♂	38.7 (37.4-39.3) ±0.77	16.9 (16.5-17.2) ±0.32	15.0 (14.6-15.2) ±0.21	10.7 (10.5-11.0) ±0.21	3.9 (3.8-4.1) ±0.11	9.0 (8.8-9.2) ±0.13	5.8 (5.6-5.9) ±0.11	7.7 (7.1-8.1) ±0.35
AMNH 236706 ♀	38.4	16.1	14.3	10.4	3.8	8.6	5.7	7.5
AMNH 236707 ♀	38.5	16.3	14.4	10.3	3.7	8.7	5.4	7.6

Molossus molossus verrillii J. A. Allen

Specimens examined (14).—2 km N, 2 km E Lebrun, 1 (TTU); 3 km S Beaumont, 4 (TTU); Charlier, 9 (AMNH).

Comparison of measurements of cranium and forearm of our series (Table 4) with values from specimens from elsewhere in the Caribbean and the South American mainland (Husson, 1962; Smith and Genoways, 1974) indicates that the Haitian bats can be referred to *M. molossus*. Relationships of Antillean and South American populations of this species to Central American and Mexican forms of *Molossus* remain problematical.

The bats from Charlier were netted shortly after sundown over a stagnant pool. Houses are present in the vicinity.

Two females taken on 21 December and five females taken on 24 August were not pregnant. Length of testes in seven males caught on 21 December averaged 3.9 mm (range, 2–5).

DISCUSSION

On the basis of their studies of species at several different localities in Costa Rica and Panamá, Fleming et al. (1972) distinguished four different reproductive patterns in tropical bats—1) seasonal monoestry (characteristic of insectivores), 2) seasonal polyestry (two distinct birth peaks, characteristic of frugivores), 3) extended season with short inactive period (characteristic of *Myotis nigricans*), and 4) year-round activity (characteristic of vampires). Even in tropical situations production of young appears to be adjusted through evolution to coincide with times of maximum availability of food.

Our reproductive data on most Haitian insectivorous species are so incomplete that comparison with mainland bats is not worthwhile, except to point out that *Macrotus waterhousii* shows reproductive inactivity in August and January and a high rate of pregnancy in May. Apparently, it is seasonally monoestrous.

Substantial numbers of female *Artibeus jamaicensis* are pregnant in December–January and in May, both in Haiti and on the mainland. In August, however, many Haitian females are also visibly pregnant, whereas in the mainland populations the embryos are in a period of delayed development and are not detectable by gross dissection (Fleming, 1971; Fleming et al., 1972). Absence of visible embryos in August is also usual for most other Panamanian and Costa Rican stenodermines (Fleming et al., 1972). In Haiti, however, many females of *Phyllops haitiensis* show measurable embryos in August (as well as in May and January). We believe that Haitian stenodermines may not show the seasonal bimodal polyestry characteristic of mainland stenodermines.

Glossophaga soricina in Panamá shows the bimodal polyestry

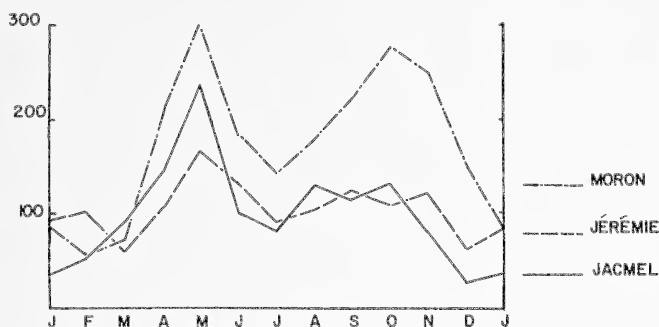


Fig. 2.—Average monthly rainfall in mm at three localities in southern Haiti. Values for Jérémie and Jacmel are 14-year averages; for Moron, nine-year averages. Data are from Woodring et al., 1924.

characteristic of other frugivorous species in Central America (Fleming et al., 1972). According to our data, the closely related *Monophyllus redmani* in Haiti does not show this pattern, as pregnant females were found only in May. Buden (1975) however reported pregnant females from Hispaniola taken in December and February. Our specimens of phyllonycterines taken in January and August include no pregnant females, but pregnant females of *Phyllonycteris* were taken in December. Young are apparently born in late spring or early summer elsewhere in the Antilles in *Erophylla* and *Phyllonycteris* (Walker et al., 1964: 320–321). Neither *Monophyllus* nor the phyllonycterines in the Antilles appear to show bimodal polyestry, and they may be seasonally monoestrous.

Although we lack 12-month data on reproduction of Hispaniolan species, we can conclude that some Antillean frugivorous bats differ reproductively from close relatives on the Central American mainland. These reproductive differences may be related through long-term evolution to differences in seasonality of abundance of food (on which we have no data) and indirectly to differences in rainfall patterns. In Costa Rica and Panamá the marked wet and dry seasons are associated with yearly bimodality in availability of fruit (Fleming et al., 1972). In Haiti there are no marked single wet and dry seasons, but rather two wet seasons (which are not very wet) separated by moderate dry seasons (Fig. 2). It is possible that the pattern of rainfall in Haiti leads to a more even production of fruit throughout the year, and allows more or less continuous reproduction of stenodermine bats. In west central Colombia, where fruit is continuously available, *Artibeus lituratus* breeds throughout the year (Tamsitt and Valdivieso, 1963).

Artibeus jamaicensis feeds primarily on ripe fruit, but some flower products, leaves, and insects may also be eaten (Gardner, 1977). *Artibeus* was observed feeding heavily on fruit of the trumpet tree (*Cecropia peltata*) at Paillant. This tree grows commonly in deforested areas in the Antilles, and in Jamaica flowers and fruits sporadically throughout the year (Adams, 1972). *Artibeus* in Haiti probably eats cultivated fruit also. Feeding habits of *Phyllops haitiensis* are unknown, but the bat is thought to feed primarily on fruit (Gardner, 1977). Haitian *Artibeus* and *Phyllops* differ in weight by a factor of 2:1, a ratio expected in insular species competing for the same general food resource. In lowland Panamá, in contrast, the canopy frugivore guild is filled by six species of stenodermines which differ incrementally by a weight factor of 1.44 (Bonaccorso, 1975). Feeding habits of *Monophyllus redmani* are not known, but it probably eats pollen, insects, and stages of fruit not used by stenodermines, as do other glossophagines (Howell, 1974). Stomachs of five Haitian specimens of *Monophyllus* taken in January contained plant material, and two of these contained insects in addition. Cuban phyllonycterines feed primarily on pollen but also eat soft fruit pulp, nectar, and insects (Silva Taboada and Pine, 1969: 15). Reproduction in *Monophyllus* and the phyllonycterines may be adjusted to seasonal availability of insects or flowers or both, and the difference in food requirements may account for the differences in reproductive biology observed between Haitian stenodermines on the one hand and *Monophyllus* and the phyllonycterines on the other.

The bat faunas of the Greater Antilles are depauperate compared to those of the mainland and of the islands on the continental shelf. Koopman (1958: 436) suggested that past environmental changes on the islands led to extinction of some species, and that water barriers prevented immediate recolonization. Empty niches would be present on the islands for some time. Niche expansion could occur in surviving species (see Lister, 1977, on niche expansion in species of Antillean *Anolis*, and Lack, 1976, on birds), an event which could hinder establishment of new colonizers. Hispaniola is a large island and is ecologically diverse in comparison with the other islands. Unfortunately we lack information on composition of its bat fauna in the Tertiary and early Quaternary, and detailed information on niche structure of its Recent bat fauna in comparison with the fauna on the mainland. Hence we cannot at this time substantiate or modify Koopman's hypothesis.

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ARTICLE 6

MICROTUS AND *PITYMYS* (ARVICOLIDAE) FROM CUMBERLAND CAVE, MARYLAND, WITH A COMPARISON OF SOME NEW AND OLD WORLD SPECIES

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ABSTRACT

Microtus guildayi, new species, *M. paroperarius* Hibbard 1944, and *Pitymys cumberlandensis*, new species, are identified in the Irvingtonian Cumberland Cave fauna on the basis of a typological and biometrical analysis of m1 and M3. *P. cumberlandensis* is the earliest known representative of *Pitymys*. Its bearing on the relationship of *Pitymys* and *Microtus* is discussed. Comparison of the Cumberland Cave *Microtus* species with other North American and European relatives leads to 1) the Middle Irvingtonian age determination of the Cumberland Cave deposits, 2) the recognition of a North American *Pedomys* lineage, and 3) the assumption of two different *Microtus* migrations from Eurasia to North America during the Middle Irvingtonian (= Early Biharian). The dental evolution in *Microtus* (*Pedomys*) and in the early *Microtus* lineages of Europe is compared. The classifications and the phylogenetic reconstructions of Biharian *Microtus* species suggested by Chaline (1972) and Van der Meulen (1973) are discussed.

INTRODUCTION

The Pleistocene Cumberland Cave locality near Cumberland, Maryland, has been known since 1913, when Dr. J. W. Gidley published his preliminary report. A monograph on the fauna, including a compilation of previous studies, was finished by Dr. C. Lewis Gazin after the death of Dr. Gidley (Gidley and Gazin, 1938). Recently Guilday (1971) discussed the Cumberland Cave fauna in his survey of the Pleistocene history of the Appalachian mammal fauna. In this discussion a number

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of additions to Gidley and Gazin's faunal list were given as a result of collecting by Carnegie Museum field parties during the 1960's, which greatly enlarged the collections of smaller mammals.

Included in this new material were the *Microtus* molars, which Guilday discussed in an unpublished contribution to the Hibbard Symposium at Ann Arbor in 1974. Gidley and Gazin (1938) recognized a single *Microtus* species, *M.* (or *Pitymys*?) cf. *involutus* Cope. Guilday noted the presence of at least two distinct m1 morphotypes, a three- and a four-triangled one. He emphasized the difficulties in separating and determining the *Microtus* species on m1's (first lower molars) but remarked: "the 4-triangle m1, whatever its taxonomic affinities, serves as a reliable index fossil in Appalachian cave faunas."

His interest being raised but lacking the time to continue the research himself, Guilday kindly invited the present author to study *Microtus* and *Pitymys* in the Carnegie Museum collections from Cumberland Cave.

The large quantity and the comparable morphology of the Cumberland m1's permitted the application of the biometrical analysis that was introduced in a study of Middle Pleistocene *Microtus* m1's from Europe (Van der Meulen, 1973). Material of the earliest North American *Microtus* representative (unnamed) and of the later *Microtus llanensis* Hibbard, *M. paroperarius* Hibbard, and *M. meadensis* Hibbard from midwestern localities has also been measured. Thus, objective comparisons between the examined North American and European species are possible.

Furthermore, the author was given ample opportunity to study dentitions of the living North American representatives of *Microtus* and *Pitymys* [throughout this paper a distinction is made between *Pitymys* and "Pitymys." *Pitymys* stands for the author's restricted use of the taxon, "Pitymys" for the common use in the literature (see section on the systematics of *P. cumberlandensis*).], not only those of the Carnegie Museum but also of other museums.

In the following sections the biometrical methods will be applied to separate the Cumberland Cave species. After the descriptions of each of these three species follow taxonomic remarks and comparisons with related forms from North America and Europe. Then the biostratigraphical implications for the American localities from which the compared *Microtus* species come, and intercontinental correlations are discussed.

The Middle Pleistocene evolution of *Microtus* in Europe, as interpreted by the author, will be compared to that in North America. Finally, Chaline's (1972) interpretation of early *Microtus* evolution is discussed in order to clarify the confusing differences between Dr. Chaline's and the author's concepts on this matter.

ACKNOWLEDGMENTS

I am greatly indebted to John Guilday and Mary Dawson of the Carnegie Museum for offering me the opportunity to revise the Cumberland *Microtus* and *Pitymys* and for their continued help and advice during the author's stay at Pittsburgh. The author gratefully profited from discussions on North American Pleistocene stratigraphy and *Microtus* systematics with Dr. Gerald Smith, University of Michigan, and with Dr. Holmes Semken and his collaborators at the University of Iowa. The author thanks Hans de Bruijn, Utrecht, Mary Dawson, John Guilday and Holmes Semken for critically reading the manuscript. Thanks are further due to the following persons and institutions who made specimens available: American Museum of Natural History, Dr. R. Teford; Carnegie Museum of Natural History, C. A. Heppenstall and Dr. D. Schlitter; Department of Biological Sciences, University of Alaska, Dr. R. D. Guthrie; Department of Biology, Fairleigh Dickinson University, Dr. R. A. Martin; Department of Geology, State University of Iowa, Dr. H. Semken; Museum of Paleontology, University of Michigan, Dr. G. R. Smith; United States National Museum of Natural History, Smithsonian Institution, Dr. C. Ray.

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METHODS AND MATERIALS

Material Studied

Six hundred and eighty-eight *Microtus* and *Pitymys* specimens in the Cumberland Cave collection of Carnegie Museum (CM) have been studied. The collection was made by Allen McCrady and Harold Hamilton and party in 1968. The specimens are numbered partly individually, partly as samples. They include all 208 upper third molars (M3's) of sample CM 20416. The remaining 480 specimens are either isolated m1's (first lower molars) or m1's in lower jaws accompanied or not with m3 and/or m2. Only a minority of the lower jaws and isolated m1's had received a preliminary assignment. Although not all available material (not counted) has been studied, it is safe to assume that a representative collection of m1 and M3 has been seen. Measurements were carried out on the 219 m1's catalogued as CM 20412, which may be regarded as an unbiased sample of the total of *Microtus* and *Pitymys* m1's according to Guilday (personal communication).

The small collection of *Microtus* and *Pitymys* from Cumberland Cave in the United States National Museum of Natural History (USNM), Washington, D.C., consists of the six lower jaws and one m1 published in Gidley and Gazin (1938) as *Microtus* (or *Pitymys*?) cf. *involutus* (Cope).

All *Microtus* material from Conard Fissure, Arkansas, collected by Dr. Russell W. Graham in 1969–1971 and stored in the paleontological collections of the State University of Iowa (SUI), has been studied. The material is part of Dr. Graham's thesis (1972) on the Conard Fissure fauna and has been determined as *M. (Pedomys) llanensis* Hibbard (55 m1's) and *Microtus paroperarius* Hibbard (five m1's). All m1's were measured for this study. Two of Graham's *M. (Pedomys) llanensis* m1's are referred to *M. paroperarius* and two other to *Pitymys cumberlandensis*, new species, for reasons discussed below.

The Museum of Paleontology, the University of Michigan (UMMP), Ann Arbor, loaned material from the localities Wathena, Kentuck and the Sunbrite (Cudahy) Ash Mine in Kansas.

All *Microtus* molars from Wathena in the UMMP collection have been seen. The collection was made by Howard O'Connor, Bob Carr and Claude W. Hibbard in 1969 from two different silt beds below the Nickerson till exposed in a pit south of Wathena, Doniphan Co. The lower silts yielded 17 m1's, the upper silts three m1's. Only the 17

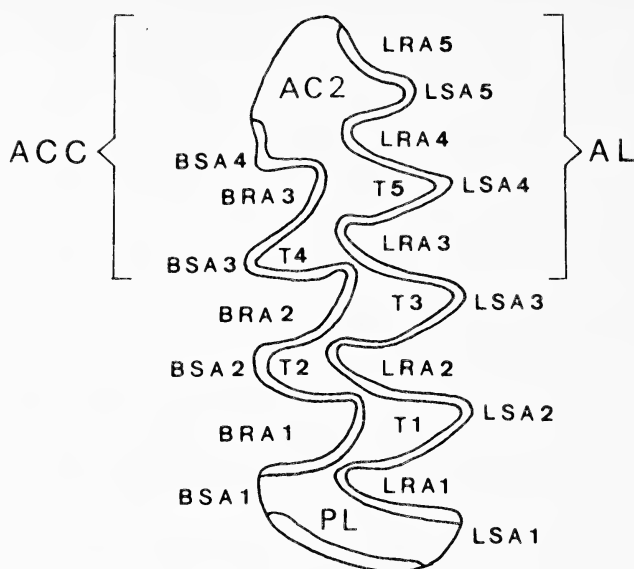


Fig. 1.—Occlusal surface of left m1 of *Microtus* showing the terminology of parts of the occlusal surface after Van der Meulen (1974). AC = anterior cap; ACC = anteroconid complex; AL = anterior loop (European context); B = buccal; L = lingual; PL = posterior lobe; RA = re-entrant angle; SA = salient angle; T = triangle.

m1's from the lower silts are used in the statistical analyses. The fauna from Wathena has been described by Sudi D. Einsohn (1971). She determined the *Microtus* molars as *Microtus llanensis* Hibbard. The greater part of her material is in the University of Kansas Natural History collection, and has not been studied by the author.

Approximately half of the *Microtus (Pedomys) llanensis* collection from Kentuck (Hibbard, 1952) could be studied. It included 15 measurable m1's.

Seventy seven unidentified *Microtus* m1's and 135 measurable m1's of *M. ("Pitymys") meadensis* Hibbard have been studied from the Sunbrite Ash Mine, which locality has yielded a great part of the so-called Cudahy local fauna (Hibbard, 1944). Seventy m1's of the unidentified *Microtus* appear to belong to *M. paroperarius*, seven m1's to *M. meadensis*. The Sunbrite Ash Mine is the type locality of both species. The material of the third Cudahy *Microtus* species, *M. (Pedomys) llanensis*, was on loan and could not be studied.

Dr. Robert A. Martin donated to Carnegie Museum a small collection of *M. (Allophaiomys)* cf. *A. pliocaenicus* Kormos from the Java local fauna, South Dakota (Martin, 1973, 1975). Although seen by the author, the Java material is not used in the statistical analyses, because it is presently under study by Dr. Martin.

Dr. R. D. Guthrie kindly sent some material of *Microtus deceiverensis* from the Cape Deceit fauna, Alaska (Guthrie and Matthews, 1971).

Terminology of Vole Molars

Upper and lower molars are designated as M and m, respectively. The terminology for the various parts of the molars is after Van der Meulen (1973, 1974). Salient angles

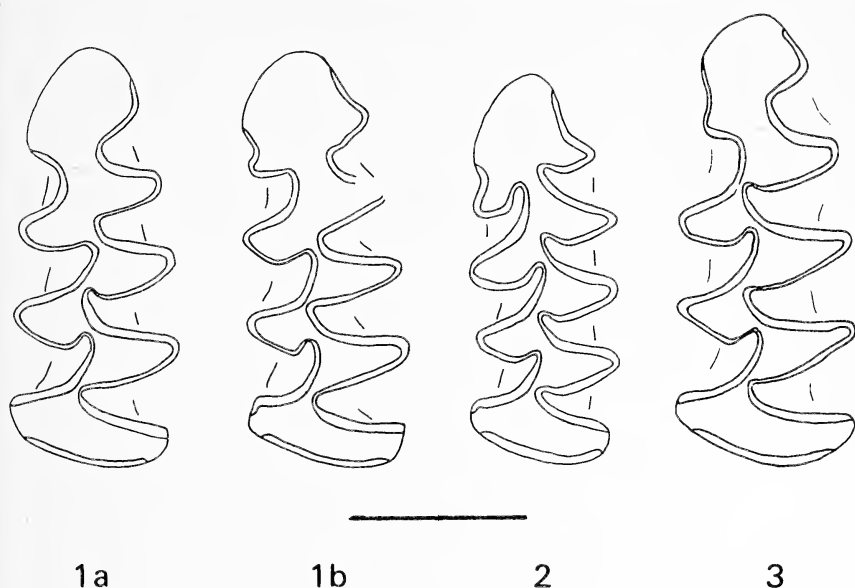


Fig. 2.—Occlusal surfaces of four left m1's of *Microtus* and *Pitymys* from Cumberland Cave illustrating the morphotypes. 1a = morphotype 1a; 1b = morphotype 1b; 2 = morphotype 4; 3 = morphotype 2.

(SA), reentrant angles (RA), and triangles (T) are counted from posterior to anterior in lower molars and reversed in upper molars. The first two triangles behind the anterior loop are numbered T1 and T2 in M1, but T2 and T3 in M2 and M3, so that homologous triangles in the upper molar series receive the same number. The terminology of the elements of the occlusal surface of m1 is given in Fig. 1. It is noted that a number of American authors use the term anterior loop for the part of m1, that is called anterior cap in the terminology used here. European authors denote as anterior loop the entire anterior dentine field of which the cap forms the anteriormost part.

Observations and Parameters for Quantitative Analysis

The microtine species of Cumberland Cave are distinguished by the m1, the relatively rare lower jaws provide some information on the morphology of associated m2's and m3's. These m2's and m3's will be described under the species description. M1 and M2 have not been studied. The patterns are all normal for *Microtus*. *Pitymys* M1 and M2 might have been separated on thickness of enamel.

The object of study is the enamel pattern of the occlusal surface of m1 and M3. The first lower molar is the best single available tool for distinguishing fossil vole species. This is confirmed by observations from living species, in which clearly different m1 patterns characterize different species. On the other hand, closely related species, of *Microtus* in particular, do not always differ in m1 patterns. This implies that paleontologists may not recognize all fossil vole species, an unknown number of the taxa containing possibly more than one species.

Time and again the great variability of the diagnostic anteroconid complex of m1 has been emphasized in the literature. This difficulty can, however, be met by adopting high

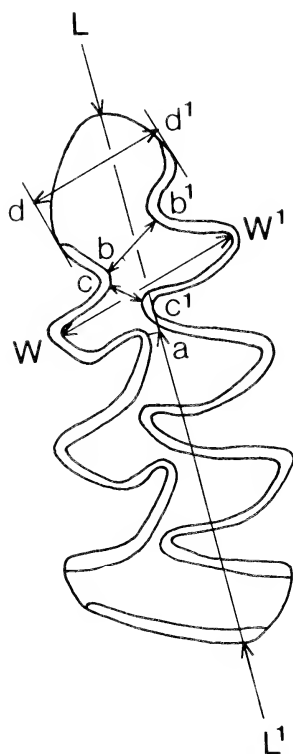


Fig. 3.—Occlusal surface of a left *Microtus* m1 illustrating the measurements. $L-L' = L$; $a-L = a$; $W-W' = W$; $d-d' = w$; $b-b' = b$; $c-c' = c$. The ratio $A/L = 100 a/L$ is a measure for the relative length of anteroconid complex; the ratio $W'/W = 100 w'/W$ for the relative width of the anterior cap; the ratio $B/W = 100 b/W$ for the degree of confluency between anterior cap and triangles 4 and 5; the ratio $C/W = 100 c/W$ for the degree of confluency between triangles 4 and 5.

confidence levels in statistical tests of differences between samples. The great variation certainly discredits a typological approach.

Morphology of m1

Lower first molars from Cumberland Cave are divided into three groups characterized by three different morphotypes (Fig. 2) numbered 1, 2 and 4 to achieve standardization with those in Van der Meulen (1973).

Morphotype 1 has an occlusal surface consisting of a posterior loop, three closed triangles and the anteroconid complex (ACC) consisting of a single dentine field. The lingual salient angles are deeper than the buccal ones; the reentrants are wide, two of them (BRA3 and LRA4) are shallow. In the middle of the posterior part of the reentrants there is usually a definite bend in the enamel. The enamel is clearly thinner on the posterior margin of all salient angles than it is on the anterior margin.

This morphotype is the same as morphotype 1 in Van der Meulen (1973), and, likewise, a distinction can be made between a more simple type 1a (Fig. 2, 1a) with broadly confluent parts of the ACC and with rounded AC2, and a more advanced type 1b (Fig. 2, 1b) in which the AC2 bears incipient salient and/or reentrant angles and one or more of the ACC parts (T4, T5 and AC2) may have narrow connections.

Morphotype 2 is characterized by the ACC being divided in two or, rarely, three fields. As a result there are four or five closed triangles. The AC2 is usually provided with two, more or less pointed, salient (BSA4 and LSA5) and shallow reentrant angles. In all other characters morphotype 2 resembles morphotype 1. This morphotype is the same as morphotype 2 as defined in Van der Meulen, 1973.

Morphotype 4 shows three closed triangles and an ACC consisting of a single field (Fig. 2, 2). It is distinguished from morphotype 1 and 2 by a) having thick enamel, which is thinner only at the tip of the reentrants, b) smaller lingual salient angles as a result of which lingual and buccal salient angles have almost the same width, c) narrow reentrants of which the posterior parts only rarely show a definite bend in the enamel, and d) a deep BRA3 and LRA4 of which the tips point more or less anteriorly.

The connections between the parts of the ACC are often narrow, and AC2 usually bears a well-developed BSA5 and LSA5 and an incipient BRA4 and LRA5. This morphotype is not known from the Middle Pleistocene of Europe.

All *Microtus* m1's from Wathena and Kentuck belong to morphotype 1. Type 1b is rare. In contrast, type 1b is more common relative to type 1a in the morphotype 1 group from Cumberland Cave. The *M. (Pedomys) llanensis* m1's from Conard Fissure virtually all belong to type 1b, a few belonging to type 1a. It seems that the morphotype 1 assemblage from Cumberland Cave is intermediate between the more primitive assemblages from Wathena and Kentuck and the more advanced *M. (Pedomys) llanensis* from Conard Fissure. This morphological series is mainly based on presence and degree of development of salient and reentrant angles at the AC2.

Two specimens from Conard Fissure determined as *M. (Pedomys) llanensis* fit the characterization of morphotype 4. *Microtus paroperarius* from the Sunbrite Ash Mine and Conard Fissure belong to morphotype 2.

The *Microtus meadensis* m1's from the Sunbrite Ash Mine do not fit one of the three morphotypes. In *M. meadensis* T4 and T5 are widely communicating, whereas the anterior loop is separated. First lower molars bearing these features have been distinguished as morphotype 3 in Van der Meulen (1973) and are characteristic of the "*Pitymys*" species of the European Middle Pleistocene.

Measurements of m1

The measurements used here are consistent with those in Van der Meulen (1973) (Fig. 3). Measurement w' is introduced here for the width of the AC2 measured parallel to W. The ratio $100 w'/W = W'/W$ is a measure of the observed increase of the width of the AC2 due to addition of salient angles in the morphotype 1 series from Wathena and Kentuck, through Cumberland Cave, to Conard Fissure.

The morphotype 4 molars from Cumberland Cave are mainly characterized by thickness of enamel and shape of the salient and reentrant angles. No satisfactorily standardized measurements were found that could quantify these characteristics.

The measurements were made by a Leitz Ortholux microscope with moving stage.

Separation of the Three m1 Morphotypes from Cumberland Cave

In order to examine the reality of the three morphotypes from Cumberland Cave, 219 m1's (CM 20412) were measured. Morphological separation resulted in the determination of 96 m1's of morphotype 1, 71 m1's of morphotype 2 and 52 m1's of morphotype 4.

Fig. 4 shows the distribution of C/W values (the degree of confluency between the

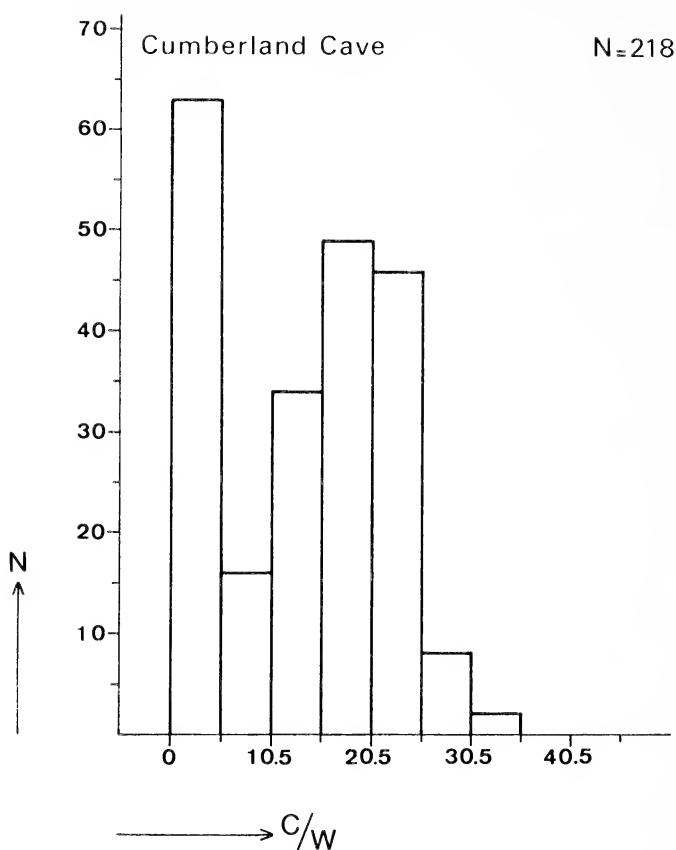


Fig. 4.—Histogram of C/W for all *Microtus* and *Pitymys* m1's from sample CM 20412, Cumberland Cave. The bimodal distribution suggests the presence of two groups.

triangles 4 and 5) of all m1's of the sample. The distribution is bimodal because of the high frequency ($N = 63$) in class $C/W = 0-5$, which is separated by class $C/W = 6-10$ with low frequency ($N = 16$) from the classes $C/W = 11-15$ through $C/W = 21-25$, again with high frequencies. The bimodality is accepted as proof that morphotype 2, that is the four-triangled form, can be biometrically isolated from the two three-triangled morphotypes. Some overlap does exist—nine m1's in class $C/W = 6-10$ and one m1 in class $C/W = 11-15$ are assigned to morphotype 2 on secondary features such as the type of enamel thickness and shape of the ACC.

As noted in the previous section no measurements were found to quantify the primary differences of morphotypes 1 and 4, but the features of morphotype 4 are clear enough to leave virtually no undetermined m1, and taxonomically important enough to permit this typological separation.

Fig. 5 shows that morphotype 1 and 4 differ clearly in their relationship between b' and w' . Morphotype 4 combines lower b values with higher w' values in comparison to

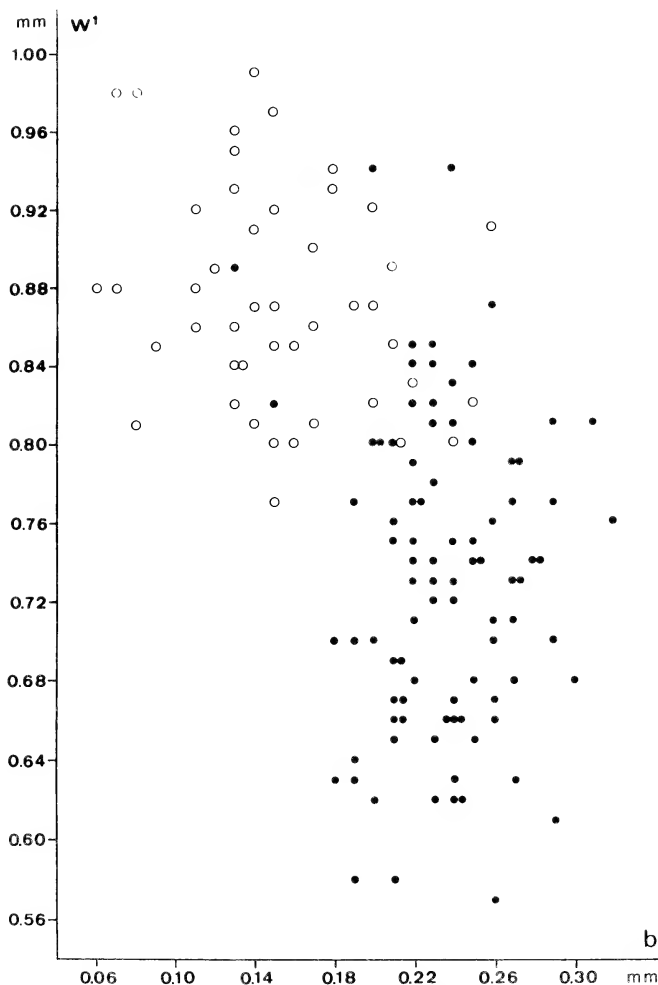


Fig. 5.—Relationship between b and w' for the morphotype 1 (*Microtus guildayi*, new species, solid circles) and morphotype 4 (*Pitymys cumberlandensis*, new species, open circles) m1's from sample CM 20412 from Cumberland Cave.

morphotype 1. This relationship is independent of the criteria used to distinguish the two morphotypes. The observed differences in this relationship, therefore, support the typological differentiation.

Other measurements will be discussed as appropriate in the systematic discussion of the Cumberland species—*Microtus (Pedomys) guildayi*, new species (equals the morphotype 1 m1's), *M. paroperarius* Hibbard (equals the morphotype 2 m1's) and *Pitymys cumberlandensis*, new species (equals the morphotype 4 m1's).

Morphology of M3

A study of 208 M3's in sample CM 20416 resulted in the distinction of three different groups characterized by three morphotypes A, B and C (Fig. 6), which are based on the number of reentrant angles that contain crown cementum and the degree of differentiation of the enamel thickness.

Morphotype A is characterized by having 1) well-differentiated enamel thickness, 2) two buccal and two lingual reentrant angles filled with crown cementum, and 3) alternating triangles T2 and T3, that is, the two anteriormost triangles.

Morphotype B is characterized by having 1) very little differentiation of the enamel thickness, 2) two buccal and two lingual reentrants filled with crown cementum, and 3) almost opposed triangles T2 and T3.

Morphotype C is characterized by having two or three buccal and three lingual reentrants filled with crown cementum. In other respects, it resembles type A.

Two molars are intermediate between types A and B, and have not been determined. Ninety-seven M3's are assigned to type A, 21 to type B, and 88 to type C.

It is very likely that morphotype B M3's should be associated with the morphotype 4 m1's, because they have the thick, little differentiated enamel in common. The more simple M3's of type A are associated with the three-triangled m1's (type 1), the more complexed M3's (type C) with the four-triangled m1's by analogy with living species such as *Microtus (Pedomys) ochrogaster* and *Microtus oeconomus* with three and four-triangled m1's respectively.

The M3's have not been measured. They will be described in more detail under the species descriptions.

SYSTEMATIC ACCOUNTS

Microtus (Pedomys) guildayi, new species

Fig. 7A-I, Q-R

Holotype.—Damaged right mandible with m1-m2, Fig. 7A; CM 20333.

Figured paratypes.—Fig. 7B-I.

Horizon and type locality.—Irvingtonian Cave filling of Cumberland Cave, near Cumberland, Maryland.

Derivatio nominis.—In honor of John E. Guilday of the Carnegie Museum of Natural History, Pittsburgh, Pennsylvania.

Referred specimens.—At the Carnegie Museum—Fragmentary jaws with one or more molars: CM 20339, CM 20340, CM 20345, CM 20348, CM 20357, CM 20358, CM 20360, CM 20362, CM 20365, CM 20368–20371, CM 20379, CM 20381, CM 20385, CM 20389, CM 20390, CM 24239. Isolated m1's: CM 20397, CM 20398, CM 20401, CM 20404, CM 20405, CM 20407, CM 20408, CM 20416 (27 m1's), unnumbered (41 m1's). Isolated M3's: CM 20416 (79 M3's). At the U.S.N.M.—USNM 7772 (jaw), 12368, 12369, 12370. All specimens are from Cumberland Cave.

Diagnosis.—Medium sized *Microtus* species, with lengthened and somewhat complicated anteroconid complex; the mean of A/L equals or is greater than 44.5, but is less than 46.3; the mean of B/W equals or is greater than 23.0 but is less than 28.0; the mean of C/W equals or is greater than 20.0; the mean of W'/W equals or is greater than 76.0 but is less than 85.0.

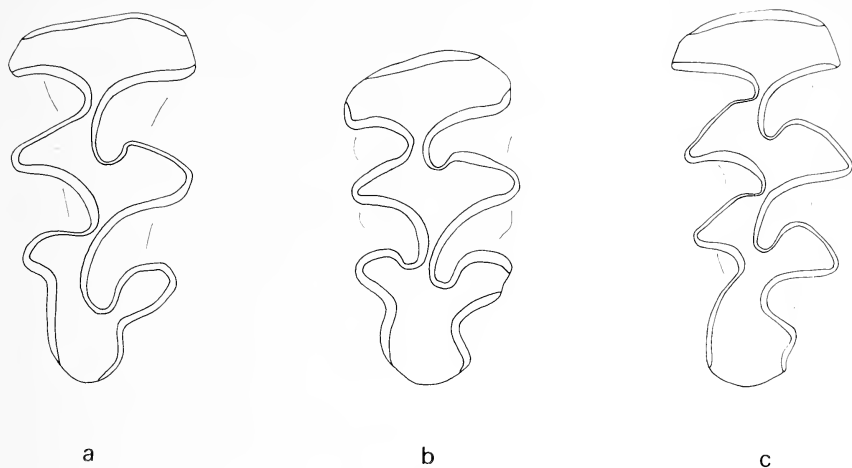


Fig. 6.—Occlusal surfaces of three right M3's of *Microtus* and *Pitymys* from sample CM 20416, Cumberland Cave, illustrating the three morphotypes—a = morphotype A; b = morphotype B; c = morphotype C.

Differential diagnosis.—*Microtus guildayi* differs from *Microtus* sp. from Wathena and Kentuck in having higher mean A/L and W'/W values and lower mean B/W and C/W values; *Microtus guildayi* differs from *Microtus llanensis* Hibbard in having lower mean A/L and W'/W values and a higher mean B/W value; it differs from *Microtus nutiensis* Chaline and *Microtus burgondiae* Chaline in having a higher mean B/W value.

Measurements.—See Tables 1, 2; Figs. 5, 8–10. Holotype: length m1–m2 = 4.53; a = 1.32, L = 2.84, W = 0.97, w' = 0.81, b = 0.20, c = 0.16, A/L = 46, W'/W = 84, B/W = 21, C/W = 16.

Description

m1.—The morphological description is based on about 200 specimens. All belong to morphotype 1 described in a previous section. The variation of the molars concerns the depth of LRA3, LRA4, and BRA3, and the shape of the anterior cap (AC2). The latter may be rounded (in some 20%), but the majority is provided with one or more incipient features (LSA5, LRA5, BSA4, BRA4). The additional reentrant angles LRA5 and BRA4 are always shallow, usually narrow, and never contain crown cementum. LSA5 and BRA4 are always shallow, usually narrow, and never contain crown cementum. LSA5 and BSA4 are well developed in 11% of the m1's (Fig. 71). The most common variants are those resembling the holotype and having an incipient BSA4 (accompanied or not with a very narrow BRA4) and a more or less rounded lingual part of the AC2.

m2.—Nineteen m1 bearing jaws of *M. guildayi* are associated with a m2. T3 and T4 are connected in all these m2's. T1 and T2 are separated in 11 m2's and slightly communicating in the remaining eight specimens.

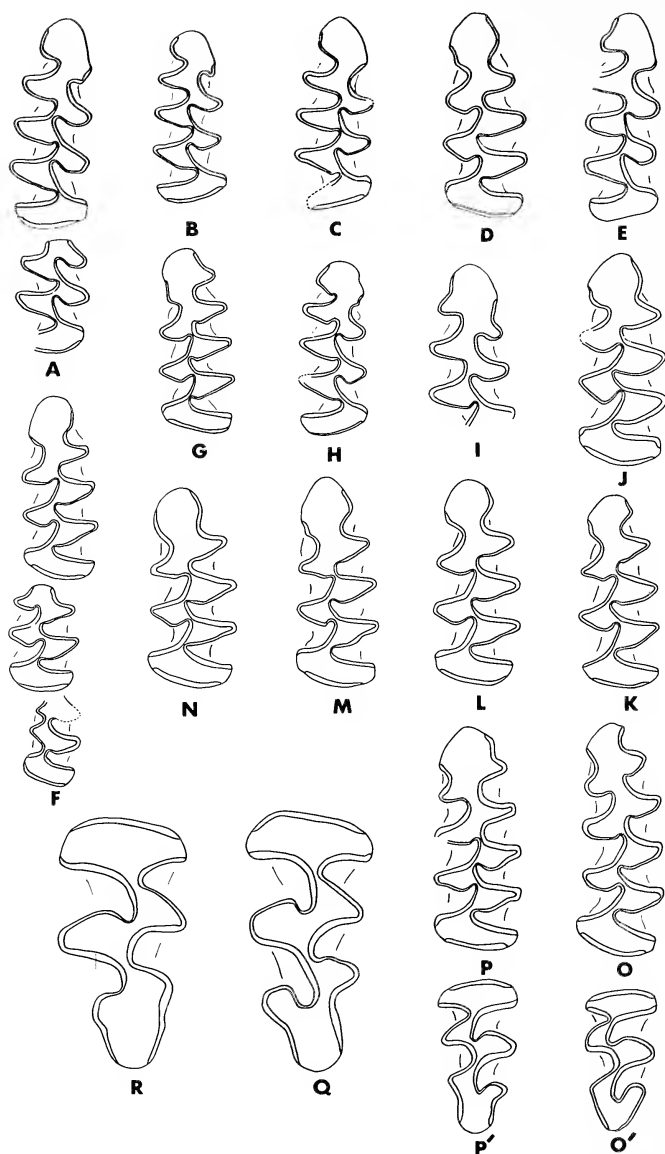


Fig. 7.—*Microtus (Pedomys) guildayi*, new species, from Cumberland Cave, Maryland—A) right m1-m2, CM 20333, holotype; B, C, E, H, I) right m1 from sample CM 20412 (PL and T1 missing in I); D, G) left m1 from sample CM 20412; F) left M1-M3, CM 20379; Q, R) left M3 from CM 20416. *Microtus (Allophaiomys)* sp. from sample Wathena, Kansas—J-L) left m1 from sample UMMP V50609. *Microtus (Allophaiomys)* sp. from sample Kentuck, Kansas—M, N) left m1 from UMMP V50516. *Microtus (Pedomys) ochrogaster* from Greenwood Co., Kansas—O, O') left m1 and right M3, CM 21529; P, P') left m1 and right M3, CM 20793.

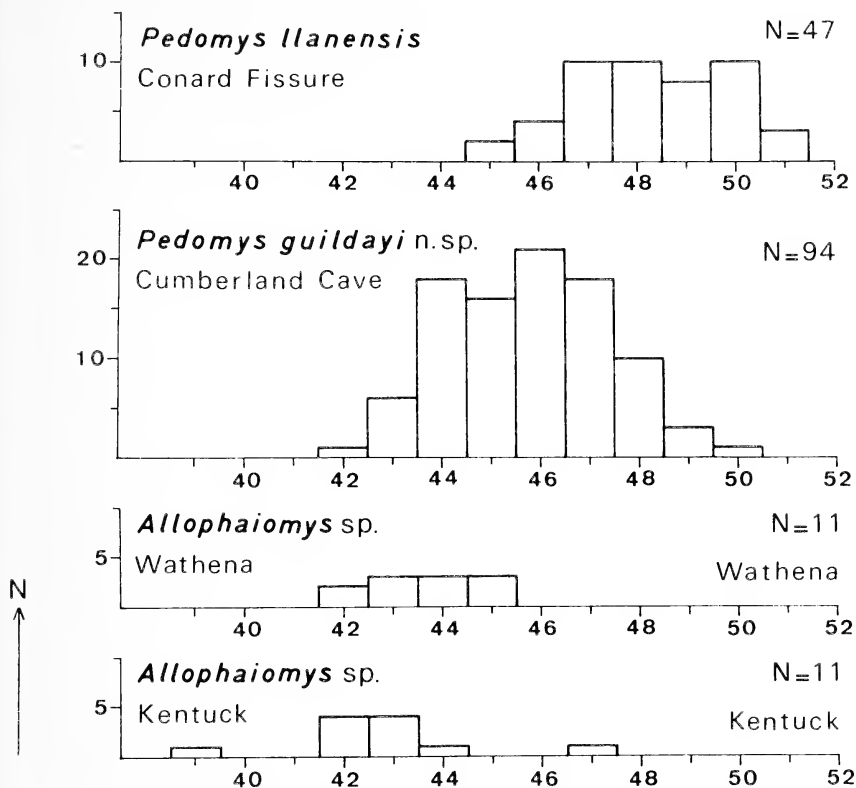


Fig. 8.—Histograms of A/L for the m1 samples of the studied *Microtus* (*Allophaiomys*) and *M. (Pedomys)* species.

m3.—The three *m3*'s that could be identified as *M. guildayi* have three dentine fields. Their BSA3 is small.

M3.—The 97 *M3*'s of CM 20416 belonging to morphotype A (see above) are determined to be *M. guildayi*. The two triangles (T2 and T3) behind the anterior loop are separated in eight specimens; in the remainder they are communicating to a greater or lesser degree (Fig. 7Q–R). Very rarely is T3 confluent with T4. The latter almost always opens into the short posterior loop. T4 and LSA3 are variably developed and may be incipient (Fig. 7R). The shallow folds at the posterior loop may be absent.

Systematic Position

Microtus guildayi fits the definition of the subgenus *Allophaiomys* Kormos, which is considered to include the fossil *Microtus* species in which the majority of m1 belong to morphotype 1 (three triangled), that is, the mean of B/W equals or is greater than eight, the mean of C/W equals or is greater than eight (Van der Meulen, 1973: 96). However,

Table 1.—Comparison of b and w' from $m1$'s of *Microtus guildayi* new species (morphotype 1), and *Pitymys cumberlandensis*, new species (morphotype 2), from Cumberland Cave (sample CM 20412).

Species	N	Mean \pm SE	SD	Range	Parameter
<i>Microtus guildayi</i>	101	0.236 \pm 0.003	0.033	0.13–0.32	w'
<i>Pitymys cumberlandensis</i>	50	0.154 \pm 0.007	0.047	0.06–0.26	
<i>Microtus guildayi</i>	90	0.730 \pm 0.008	0.080	0.57–0.94	
<i>Pitymys cumberlandensis</i>	46	0.874 \pm 0.008	0.056	0.77–0.99	

three-triangled $m1$'s are also typical of the living subgenera *Phaiomys* Blyth from Asia, *Pedomys* Baird from North America, and *Orthriomys* Merriam from Mexico. The latter monotypic (sub)genus shows a number of dental features, which it shares only with the equally monotypic *Herpetomys* from Guatemala. These features are the thin, little differentiated enamel, and the large and tightly closed triangles including T1 and T2 of $m3$. It seems to be largely a matter of taste whether *Orthriomys* and *Herpetomys* would be included in *Microtus* at all, or if they should be placed together in a separate genus.

Allophaiomys, *Phaiomys*, and *Pedomys* cannot be separated on the morphology of the dentition. One can draw an arbitrary boundary between *Allophaiomys* species and *Pedomys ochrogaster* (the only living species) on the basis of the W'/W ratio, but the difference being minor, this will hardly satisfy the paleontologist working with a purely morphological concept of taxa. On the other hand, those attempting a natural grouping of species cannot accept the uniting in a single subgenus of *Phaiomys* and *Pedomys*, which seem to have evolved independantly in Asia and North America. The present author, favoring the latter attitude, regards *Allophaiomys* as the stock group of *Microtus*, and retains the names *Phaiomys* and *Pedomys*. *Microtus guildayi*, therefore, is assigned to *Pedomys*.

In *Allophaiomys* are included the following: *Microtus deucalion* (Kretzoi); *M. pliocaenicus* (Kormos) = *M. laguroides* (Kormos), type species of *Allophaiomys*; *M. ruffoi* (Pasa); *M. nutiensis* Chaline = *M. (Allophaiomys)* sp. A in Van der Meulen (1973); *M. burgondiae* Chaline = *M. (Allophaiomys)* sp. B in Van der Meulen (1973) assigned by Chaline (1972) to the subgenus *Suranomys* Chaline, which is considered a superfluous name, since it includes *M. nivalis*, type species of the subgenus *Chionomys* Miller; *Microtus* sp. (= *Allophaiomys* cf. *A. pliocaenicus* in Martin, 1975) from the Sappa Fm., Wathena, Kentuck and Java. The following species are assigned to *Phaiomys*: *Microtus leucurus* (Blanford) type species of *Phaiomys*; *M. strauchi* Büchner; *M. carruthersi* Thomas; *M. juldaschi* (Severtzow); *M. irene* Thomas; *M. oniscus* Thomas. To *Pedomys* are assigned the following: *M. och-*

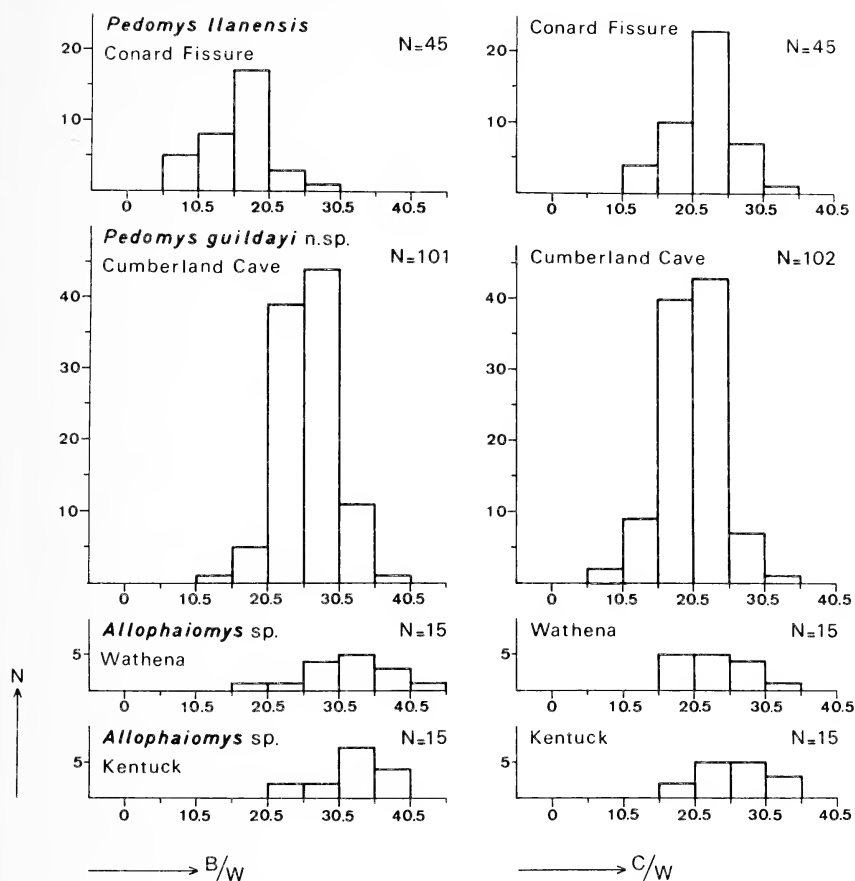


Fig. 9.—Histograms of B/W and C/W of the m1 samples of the studied *Microtus* (*Allophaiomys*) and *M. (Pedomys)* species.

rogaster Baird, type species of *Pedomys*; *M. ilanensis* Hibbard; *M. guildayi* new species. Only species seen, or adequately figured in the literature (Hinton, 1926; Ognew, 1964) have been considered.

There is a nomenclatorial problem concerning the *Pitymys involutus* Cope 1871, which is better discussed before *Microtus guildayi* is compared to other species. Gidley and Gazin (1938) noted marked similarity in morphology and close correspondence in size between their *Microtus* (or *Pitymys*?) cf. *involutus* (Cope) from Cumberland Cave and the type of *Pitymys involutus* from the Port Kennedy, Pennsylvania locality. Hibbard (1955) reviewed the Port Kennedy arvicolids

and found that the molars of the *P. involutus* holotype were missing. He, therefore, had to follow the description of Gidley and Gazin (1938), who emphasized that Cope's illustrations were incorrect. According to Gidley and Gazin the m1 of the discussed holotype was a three-triangled form resembling the living *P. pinetorum* but having a slightly simpler enamel pattern. Neither Gidley and Gazin, nor Hibbard were aware of the fact that *M. (?) cf. involutus* from Cumberland Cave includes three different species (all three being present in the USNM material studied by Gidley and Gazin), two of which have three-triangled m1's—*M. guildayi* and *Pitymys cumberlandensis*, new species. It cannot be established whether the *P. involutus* holotype resembles the *Microtus* species or the *Pitymys* species. Hibbard (1955) found only a single m1 in the existing Port Kennedy arvicolid material, which might belong to *P. involutus* judging from its size. This specimen (Hibbard, 1955: Fig. 2D) seems to belong to *Pitymys*. However, this is not sufficient evidence that the holotype was a *Pitymys* as well. Therefore, and because the Port Kennedy locality has been destroyed (Guilday, personal communication), *Pitymys involutus* Cope 1871 is considered to be a *nomen dubium* and will not be used.

Comparisons with Related North American Species

Microtus guildayi resembles the living *M. ochrogaster* in having a three-triangled m1 and a two-triangled M3. The differences concern the anterior cap of m1, which always bears two well-developed salient angles (LSA5 and BSA4) and shallow reentrant angles (LRA5 and BRA4) in *M. ochrogaster*. These features may be lacking in *M. guildayi* or, if present, are usually smaller. BRA4 in the m1 of the living species normally contains crown cementum, whereas it never does in the Cumberland Cave specimens. In the few *M. ochrogaster* M3's that have been seen, the two central triangles are separated, whereas in *M. guildayi* they are usually communicating.

Microtus llanensis m1's are characterized by the lesser development of the additional features of the AC2 in comparison to *M. ochrogaster*. Since the *M. llanensis* type material was not available, *Microtus guildayi* could only be compared to *M. llanensis* from Conard Fissure studied by Dr. Russell Graham (1972), who directly compared his material to *M. llanensis* from its type locality. He found the two m1 assemblages morphologically identical, and specifically mentioned the "trefoiled anterior loop" (anterior cap in this paper) in the Conard and Cudahy specimens. Some 10% of the *M. guildayi* m1's resemble the central variant of *M. llanensis* in having a trefoiled cap. The differences between the A/L, B/W, and W'/W distributions of *M. guildayi* and *M. llanensis* (see differential diagnosis, Table 2 and Fig. 8) are so great that testing them was considered unnecessary. It further appears that

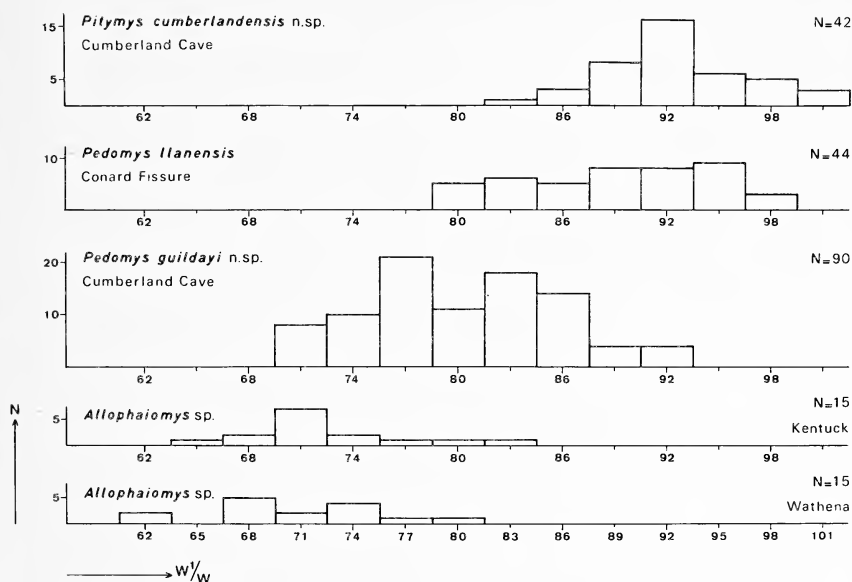


Fig. 10.—Histograms of W'/W for the m1 samples of the studied *Microtus* (*Allophaiomys*), *M. (Pedomys)*, and *Pitymys* species.

the *M. llanensis* m1's are somewhat larger than the *M. guildayi* m1's (Table 2).

Microtus molars from Kentuck and Wathena have been determined as *M. (Pedomys) llanensis* by Hibbard (1952) and Einsohn (1971) respectively. Some 20% of the *M. guildayi* resemble the majority of the m1's from Wathena and Kentuck in the presence of a rounded AC2. Although the number of observations is small, the differences (Table 2, Figs. 8–10) are considered to be large enough to separate the Kentuck and Wathena assemblages from *Microtus llanensis* and *M. guildayi* and to include them in another, probably new, species, which is referred to as *Microtus (Allophaiomys)* sp. The naming of this species falls outside the scope of this paper, which deals with part of the Wathena and Kentuck *Microtus* material only.

Allophaiomys cf. *A. pliocaenicus* from the Java local fauna is considered the same species as the one from Kentuck (Martin, 1973, 1975, and my observations). *Microtus* cf. *llanensis* from the type section of the Sappa Formation, Nebraska (Schultz and Martin, 1970; Einsohn, 1971: Pl. 8, Fig. 8), probably belongs to our *Microtus* sp., as well.

Our W'/W and B/W distributions (reflecting the relative width of the anterior cap and the communication between this cap and the fourth and fifth confluent triangles) fully confirm Graham's (1973) observation

Table 2.—Measurements and ratio data for ml's of *Microtus* sp. from Wathena and Kentuck, *Microtus guildayi*, new species, from Cumberland Cave and *Microtus llanensis* from Conard Fissure.

Locality	N	Mean \pm SE	SD	Range	Parameter
Wathena	11	2.762 \pm 0.033	0.110	2.60–2.92	L
Kentuck	11	2.852 \pm 0.052	0.173	2.55–3.10	
Cumberland	94	2.583 \pm 0.019	0.181	2.27–3.07	
Conard	47	2.724 \pm 0.026	0.176	2.32–3.26	
Wathena	11	43.6 \pm 0.34	1.12	42–45	A/L
Kentuck	11	42.7 \pm 0.57	1.90	39–47	
Cumberland	94	45.7 \pm 0.17	1.65	42–50	
Conard	47	48.3 \pm 0.23	1.58	45–51	
Wathena	15	70.7 \pm 1.19	4.59	62–79	W'/W
Kentuck	15	72.3 \pm 4.33	4.33	65–82	
Cumberland	90	80.4 \pm 0.59	5.57	70–91	
Conard	44	89.6 \pm 0.86	5.69	80–99	
Wathena	15	31.3 \pm 1.53	5.91	20–41	B/W
Kentuck	15	32.1 \pm 1.42	5.51	22–40	
Cumberland	101	26.0 \pm 0.40	3.97	13–36	
Conard	45	18.8 \pm 0.89	5.94	7–32	
Wathena	15	23.1 \pm 1.15	4.45	17–31	C/W
Kentuck	15	25.6 \pm 1.14	4.40	19–33	
Cumberland	102	20.4 \pm 0.40	4.08	9–31	
Conard	45	21.6 \pm 0.59	3.93	12–31	

that the anterior cap of "*P. llanensis* from the Kentuck Assemblage (Hibbard, 1952) is a simple crescent-shape as compared to the more trefoiled loop of the Conard and Cudahy specimens. Also the neck between the anterior loop (=anterior cap in our terminology) and the fourth and fifth confluent triangles of the Conard and Cudahy specimens is narrower than that of the Kentuck specimens." Additionally the A/L values (that is, the relative lengths of the anteroconid complex) of the Kentuck and Wathena specimens are considerably lower than those of *M. llanensis*. The Wathena and Kentuck specimens yield nearly identical distributions of the various parameters.

The A/L, W'/W, and B/W distributions of *M. guildayi* are intermediate between those of the Kentuck and Wathena specimens on the one hand and the Conard specimens on the other hand. It is concluded that *Microtus* (*Allophaiomys*) sp. from Wathena and Kentuck, *M. (Pedomys) guildayi*, *M. (Pedomys) llanensis*, and *M. (Pedomys) ochrogaster* belong to an evolutionary lineage, in which the mean of A/L and W/W' increase, while the mean of B/W decreases, reflecting the relative increase of the ACC in comparison to the total length of ml.

This is caused by the addition of new salient and reentrant angles at the anterior cap, while at the same time the communication between the anterior cap and T4 and T5 gets narrower.

This conclusion is almost entirely based on the morphology of m1. There is no independent stratigraphic control on the time sequence of the localities resulting from the assumed *Microtus* evolution, except for the fact that *Microtus* sp. from the Sappa formation comes from a level below the type S Pearlette Ash (Coleridge Ash) dated 1.2 m.y. (=million years) (Zakrzewski, 1975), and that *M. llanensis* from the Cudahy fauna is found directly beneath a type O Pearlette Ash, which has been dated as 0.6 m.y.

The changes found in the "*Pitymys*" lineage in Europe (Van der Meulen, 1975) are fully comparable to those found in the North American lineage described above, which will be referred to as the *Pedomys* lineage.

Comparisons with Related European Species

Microtus (*Allophaiomys*) sp. from Wathena and Kentuck differs from *M. (Allophaiomys) deucalion* Kretzoi in having greater differentiation in enamel thickness, and probably in the morphology of M3. The four M3's seen from Wathena, the seven M3's from Kentuck, and five M3's from the Java local fauna are of the normal *Microtus* type, whereas in *M. deucalion*, a *Mimomys*-like M3 is common (Van der Meulen, 1974). *Microtus* sp. closely resembles *M. (Allophaiomys) pliocaenicus* Kormos for which reason Martin (1975) determined the *Microtus* from Java and Kentuck as *Allophaiomys* cf. *A. pliocaenicus*. The ratios A/L and C/W are in accordance with this, but *Microtus* sp. gives mean B/W values, which are intermediate between *M. deucalion* (the mean of B/W = 36.8) and *M. pliocaenicus* (the mean of B/W = 25.3).

The morphology of *Microtus (Pedomys) guildayi* m1 comes nearest to *M. (Allophaiomys) nutiense* Chaline [= *M. (Allophaiomys)* sp. A in Van der Meulen, 1975], as far as the shape of the AC2 is concerned. *M. guildayi* differs, however, in having a lower mean A/L and a considerably higher mean B/W value than *M. nutiense*.

In general, in Europe there are no *Microtus* species with a fairly well-developed AC2 bearing salient and reentrant angles in conjunction with an anteroconid complex composed of a single dentine field, as is characteristic of *M. (Pedomys)* species.

These North American species resemble the living, central Asian species, *M. (Phaiomys) carruthersi* Thomas and, to a lesser degree, *M. (Phaiomys) juldaschi* Severtsov. In the M3 of *M. carruthersi* T2 and T3 are broadly communicating as in most *Microtus* specimens from Wathena and Kentuck and in *M. guildayi*.

The resemblances are thought to be due to parallel evolution because probable ancestors are known from both continents.

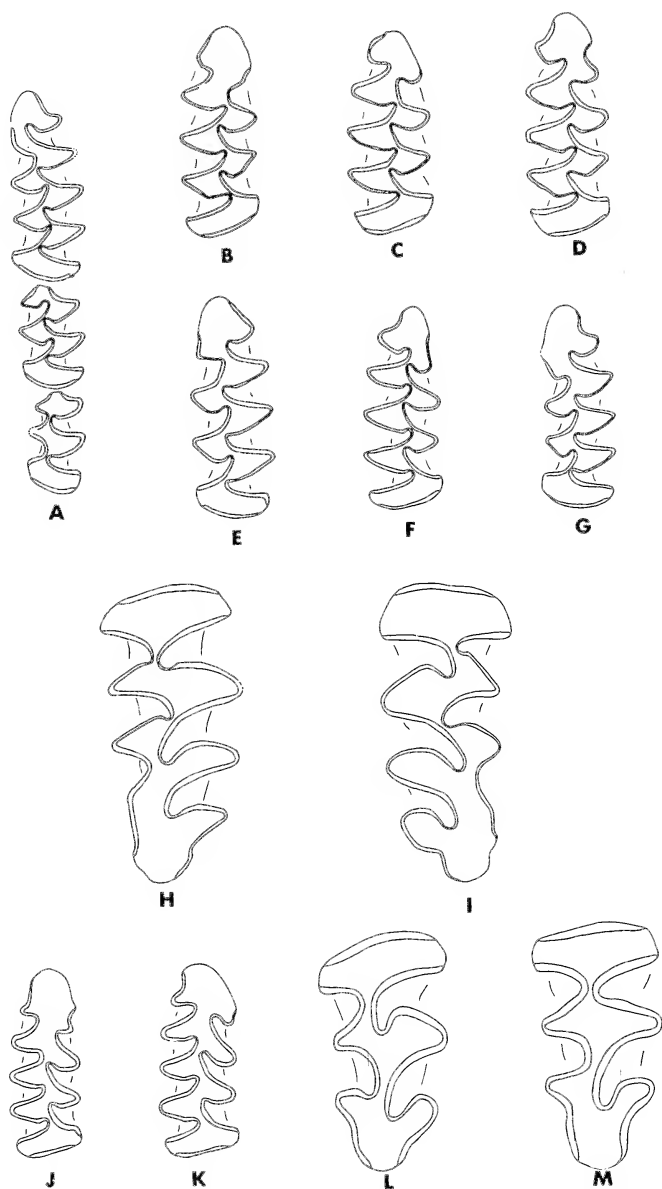


Fig. 11.—*Microtus paroperarius* from Cumberland Cave, Maryland—A) left m1-m3, CM 20347; B–D) right m1 from sample CM 20412; E, G) left m1 from sample CM 20412; F) right m1 from unnumbered sample; H) right M3 from sample CM 20416; I) left M3 from sample CM 20416. *Pitymys Cumberlandensis*, new species, from Cumberland Cave, Maryland—J) right m1 from unnumbered sample; K) right m1 from sample CM 20412; L, M) right M3 from sample CM 20416.

Table 3.—*Measurement and ratio data for Microtus paroperarius m1's from three localities.*

Locality	N	Mean \pm SE	SD	Range	Parameter
Cumberland	60	2.738 \pm 0.025	0.192	2.39–3.21	L
Sunbrite	46	2.789 \pm 0.023	0.154	2.41–3.10	
Conard	5	2.730 \pm 0.076	0.170	2.61–3.01	
Cumberland	60	48.5 \pm 0.23	1.76	45–54	A/L
Sunbrite	46	48.2 \pm 0.28	1.92	43–52	
Conard	5	48.0 \pm 0.71	1.58	46–50	
Cumberland	66	19.2 \pm 0.83	6.73	<5–36	B/W
Sunbrite	51	17.5 \pm 1.02	7.29	<5–35	
Conard	3	17.3 \pm 1.45	2.52	15–20	
Cumberland	74	<5		<5–13	C/W
Sunbrite	54	<5		<5	
Conard	3	<5		<5	

Microtus paroperarius Hibbard 1944

Fig. 11A–I

Locality.—Cumberland Cave, Maryland.

Material.—Mandible with m1–m3: CM 20356; mandibles with m1–m2 or m1: CM 20336–20337, CM 20341–20343, CM 20349–20350, CM 20353, CM 20364, CM 20367, CM 20374, CM 20376–20377, CM 20380, CM 20384, CM 20386, CM 20388; isolated m1's: CM 20396, CM 20399–20400, CM 20402–20403, CM 20406, CM 20412/106, 111, 112, 117, 118, 121–164, 166–195, CM 20416 (37 m1's), unnumbered (42 m1's); M3: CM 20416 (88 specimens). Mandible with m1–m2: USNM 12055.

Measurements.—See Table 3 and Fig. 12.

Description

m1.—Hundred eighty-five m1's of this species have been studied. The counts given below are based on the 152 morphotype 2 m1's in samples CM 20412, 20416, and an unnumbered sample. The variation of this basically four-triangled molar mainly concerns the depth of the reentrant angles shaping the AAC (and hence the number of closed triangles) and the presence or absence and shape of salient angles at the AC2.

The most common variant ($\pm 70\%$) is a four-triangled molar in which BSA4, BRA4, LSA5, and LRA5 are present. The shape of the mentioned reentrant and salient angles is variable. In the remaining 30%, one or more of these features are absent. There are four (2.5%) five-triangled (Fig. 11F) and eight (5%) three-triangled variants (Fig. 11G). In the majority of the BRA4 (90%) and LRA5 ($\pm 86\%$) crown cementum is absent.

m2.—In the nineteen jaws assigned to *M. paroperarius* (including USNM 12055) containing m2, eight m2's have communicating T1–2 and T3–4. In the remaining 11, T1 and T2 are separated and in five of these T3 and T4 are separated as well.

m3.—The single known specimen shows three dentine fields. BSA3 is fairly well developed.

M3 (see also definition of morphotype C).—Behind the AL follow three triangles and the posterior loop, which is provided with a well-developed LSA3 and a LRA3 of LSA4 of variable shape. T2 and T3 are confluent (to a variable degree) in 61 of 88 M3's of CM 20416; in 19 specimens they are almost, and in eight completely, separated.

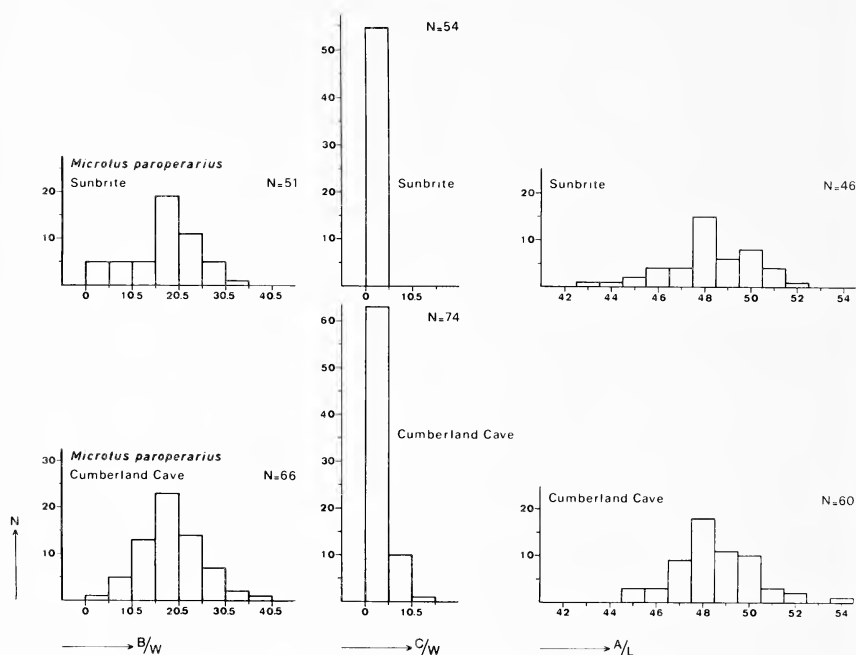


Fig. 12.—Histograms of A/L, B/W and C/W for the m1 samples of *Microtus paroperarius* from Cumberland Cave (CM 20412) and the Sunbrite Ash Mine (UMMP V40299).

Remarks

The Cumberland Cave material has been compared to topotype material of *Microtus paroperarius* from the Cudahy Ash Mine (Sunbrite). There is great resemblance between the two m1 assemblages, both in morphology and in the means and distributions of measurements and ratios (Fig. 12). Paulson (1961) notes that some 20% of the *M. paroperarius* m1's from the Cudahy local fauna are five-triangled. The 59 measurable m1's in UMMP: V40299 from Sunbrite contain 8–9% of five-triangled variants. The median test (Dixon and Massey, 1969) yielded $\chi^2 = 0.3164$ (1 df.) in the comparison of the B/W distributions of *M. paroperarius* from Sunbrite and Cumberland, not indicating a significant difference. It is possible that Paulson included some five-triangled variants of *M. meadensis* in his counts. This is concluded from the presence of seven five-triangled *M. meadensis* variants in vial V40299 (evidently picked for *M. paroperarius*). *M. meadensis* is distinguished from *M. paroperarius* by the better developed anterior loop of the former. On this criterion the *M. paroperarius* m1's of Paulson (1961: Figs. F and G) belong to *M. meadensis*. Neither Hibbard (1944)

nor Paulson (1961) have described five-triangled variants of *M. meadensis*.

Microtus paroperarius is additionally known from the Vera local fauna (Hibbard and Dalquest, 1966) and Conard Fissure (Graham, 1972). In both these localities, it is a rare species.

Guthrie and Matthews (1971) described *Microtus deceitensis* from the Cape Deceit fauna in Alaska and point out that the m1 of their species is simpler than that in *M. paroperarius*, whereas its m3 is unusual for *Microtus* because of the deep first buccal reentrant. The lengths of m1 of *M. deceitensis* range from 3.1 to 3.95 mm (Guthrie and Matthews, 1971: fig. 8), which are very high values for any *Microtus* and are much higher than those for *M. paroperarius*. The M3 associated with *M. paroperarius* are the normal three-triangled variants found in many extant species, whereas those of *M. deceitensis* are more simple (Guthrie and Matthews, 1971: 489).

Comparison to Related European Species

Hibbard (1944) noted the morphological resemblances between *M. paroperarius* and *M. ratticepoides* Hinton, 1923 from the Upper Freshwater Beds near West Runton in England. He also noted the unclear separation of *M. ratticepoides*, *M. nivalinus* Hinton, 1923, *M. nivaloides* F. Major, 1902, and *M. arvalinus* Hinton, 1923. The latter three species also have West Runton as their type locality, and at least the first three should be included in a single species—*M. nivaloides* (Van der Meulen, 1973). Pending a revision of *Microtus* from West Runton the author distinguished *Microtus* sp. C from Villány-8 and *Microtus* sp. D from Villány-6 in Hungary (Van der Meulen, 1973). The latter contains more five-triangled variants than the former, which predominantly consists of four-triangled *M. ratticepoides* variants. *M. paroperarius* resembles *Microtus* sp. C both in size and morphology, and differs only in a higher mean A/L value. The median tests on the differences between the A/L distributions of *M. paroperarius* from Cumberland Cave and Cudahy and *Microtus* sp. C from Villány-8/10 yielded $\chi^2 = 16.499$ and $\chi^2 = 15.936$, respectively. These χ^2 values largely exceed $\chi^2_{99\%} = 6.635$ (1 df.).

Both *Microtus* sp. C and *M. paroperarius* closely resemble the living species *M. oeconomus* (= *M. ratticeps*) in Eurasia and *M. operarius* in North America. The specific separation (if correct) of the living (Ognev, 1964) and fossil species is not reflected in their dental morphology, except that only in *M. paroperarius* M3, T2, and T3 are often communicating.

Microtus deceitensis is unique in size and in its combination of dental characters of m1, m2, and M3. It apparently constitutes an early side branch of *Microtus* evolution, and cannot, in my opinion, be re-

Table 4.—*Measurement and ratio data for m1's of Microtus meadensis from the Sunbrite (Cudahy) Ash Mine, Kansas.*

Parameter	N	Mean \pm SE	SD	Range
L	99	2.883 \pm 0.016	0.156	2.45–3.40
A/L	99	53.4 \pm 0.17	1.67	48–58
B/W	117	<5.5		0–5
C/W	117	18.7 \pm 0.45	4.88	3–30

garded to be the ancestor to *M. paroperarius* or *Microtus* sp. C, as thought by Guthrie and Matthews (1971). The more probable ancestor to these species is the predominantly three-triangled *Microtus burgondiae* Chaline (1972) = *Microtus* sp. B, Van der Meulen (1973), which has a more complicated AC2 than the four-triangled *M. deceitensis*.

With this interpretation of *M. deceitensis*, there is no other North American vole species left that can be considered to be intermediate between *Microtus* sp. from Wathena and Kentuck and *M. paroperarius*. It is assumed that *M. paroperarius* is another Eurasian immigrant, directly descending from *Microtus* sp. C (see below).

Comparison of Microtus meadensis Hibbard and Microtus arvalidens Kretzoi

Associated with *Microtus paroperarius* and *M. llanensis* from the Cudahy fauna is *M. meadensis*. Hibbard (1944) in his original description noted the resemblance of *M. meadensis* m1's with those of *M. arvalidens* (=“*Pitymys*” *arvaloides* Hinton), which is known from many Middle Pleistocene localities in Europe and is often associated with *Microtus* sp. C. Although Hibbard placed *M. meadensis* in the subgenus “*Pitymys*,” he notes after comparisons with *P. nemoralis*: “The patterns of m1 and m2 of *Pitymys meadensis*, *P. arvaloides* and *P. gregaloides* seem more closely related to the living genus *Neodon* of southeastern central Asia than to our living forms of *Pitymys*” (Hibbard, 1944: 732). In the present paper, it is confirmed that *Microtus meadensis* and *M. arvalidens* are not related to the living American *Pitymys* (see section on the taxonomy of *Pitymys*). *Microtus meadensis* is largely different from the probably slightly older *Pitymys cumberlandensis*, new species, from Cumberland Cave and the contemporaneous or slightly younger *P. cumberlandensis* from Conard Fissure (see below).

One hundred thirty-seven measurable m1's (UMMP V43938) of *M. meadensis* from its type locality, the Sunbrite Cudahy Ash Mine (Univ. of Kansas Locality 17), have been studied (Table 4) and compared to *M. arvalidens* from Nagyharsányhegy-4 and Villány-6 in

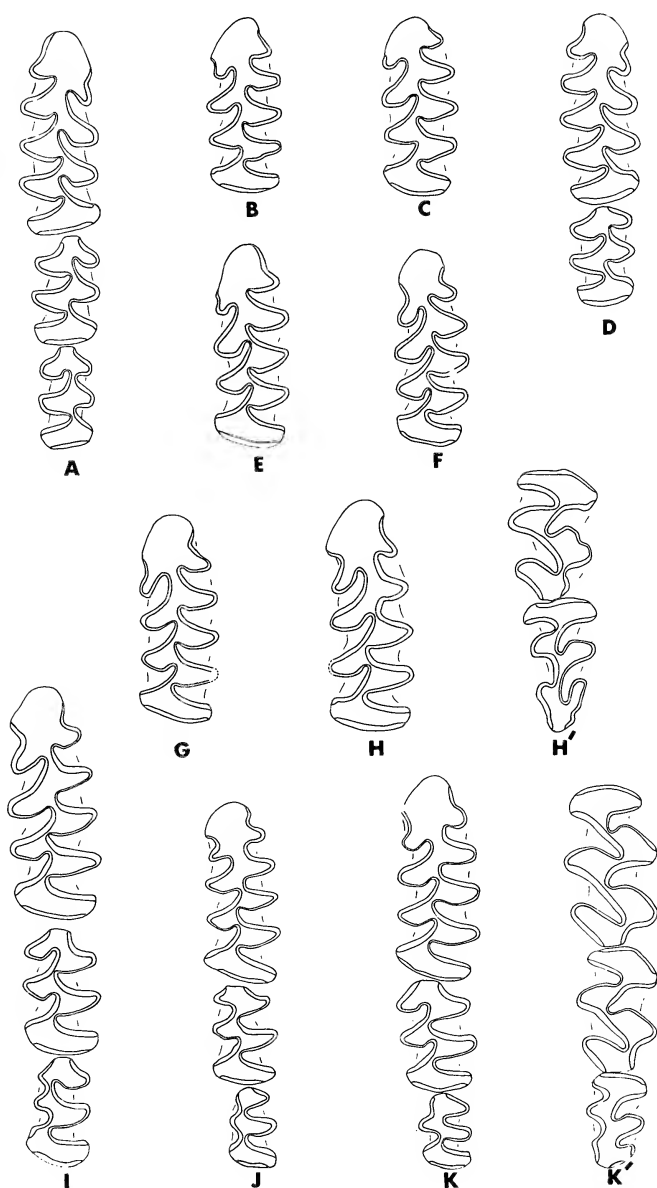


Fig. 13.—*Pitymys cumberlandensis*, new species, from Cumberland Cave, Maryland—A) right m1-m3, CM 20338, holotype; B) left m1 from unnumbered sample; C, E–G) left m1 from sample CM 20412; D) right m1-m2, CM 20378. *Pitymys pinetorum scalopsoides* from Lawrence Co., Pennsylvania—H, H') left m1 and right M2-M3, CM 26727. *Pitymys pinetorum nemoralis* from Adair Co., Oklahoma—I) left m1-m3, USNM 87253, topotype. *Pitymys pinetorum pinetorum*—J) left m1-m3, USNM 276510. *Pitymys pinetorum parvulus* from Ocala, Florida—K, K') left m1-m3 and right M1-M3, USNM 210487.

southern Hungary. The mean of L of m1 of *M. meadensis* is larger than that of the European assemblages. The mean of A/L (relative length of the anteroconid complex) of the former is somewhat larger than that found for the *M. arvalidens* from Villány-6, its mean of C/W (communication between T4 and T5) value is somewhat smaller. The differences with *M. arvalidens* from Nagyharsányhegy-4, which is somewhat more primitive than *M. arvalidens* from Villány-6, are greater. The figures confirm Hibbard's observation of the close resemblances between *M. meadensis* and *M. arvalidens*.

***Pitymys cumberlandensis*, new species**

Figs. 11J–M, 13A–G

Holotype.—Damaged, right mandible m1–m3, Fig. 13A; CM 20338.

Figured paratypes.—Fig. 11K; Fig. 13C, E–G.

Horizon and type locality.—Irvingtonian cave filling of Cumberland Cave, near Cumberland, Maryland.

Derivatio nominis.—Named after the type locality.

Referred specimens.—From Cumberland Cave collection at Carnegie Museum—Fragmentary jaws with one or more molars: CM 20334, CM 20335, CM 20344, CM 20346, CM 20361, CM 20363, CM 20378, CM 20382, CM 20393, CM 24245, CM 24263–24264; isolated m1's: CM 20409–20410, CM 20416 (9 m1's), no number (14 m1's); isolated M3's: CM 20416 (21 M3's). From Cumberland Cave collection at USNM—USNM 12602. From Conard Fissure collection at the State University of Iowa—SUI 35727-B, no. 1; SUI 35736/L.

Diagnosis.—A *Pitymys* species with molars that show very little differentiation of the enamel thickness and with m1 in which BRA4 and LRA5 are shallow and rarely contain crown cementum, and with unreduced m3 and M3.

Differential diagnosis.—*Pitymys pinetorum* and *P. parvulus* have a more reduced m3 and M3 than *P. cumberlandensis*. *P. pinetorum scalopsoides* m1's have better developed reentrant angles on the anterior cap than *P. cumberlandensis*. The molars of *P. nemoralis* have more differentiated enamel, whereas the communication between AC2 and T4–T5 is narrower than in *P. cumberlandensis*.

Measurements.—See Table 1, 5. The holotype: m1–m3 = 5.31; a = 1.24, L = 2.60, W = 0.97, w' = 0.87, b = 0.14, c = 0.12, A/L = 48, W'/W = 90, B/W = 14, C/W = 12.

Description

m1.—The description of m1 is based on 90 specimens. The occlusal surface shows an enamel pattern of a PL, three triangles, and a fairly complicated ACC consisting of two triangles (T4 and T5) and a broad AC2, which is usually bearing well-developed BSA4 and LSA5 and incipient BRA4 and LRA5. Narrow communications are regularly present between T1, T2, and T3. The communication between T1 and T2 may be broad. The enamel is thick. Its thickness is normally reduced at the anterior parts of the reentrants. The reentrant angles are narrow and deep. The buccal ones are almost as deep as the lingual ones. The tips of the salient angles are not pointed in most specimens. Two out

of the 67 specimens of CM 20416, 20412, and an unnumbered sample have crown cementum in LRA4, one in BRA4, and two in both reentrants.

m2.—All 11 *m2*'s associated with *P. cumberlandensis* *m1*'s consist of three dentine fields.

m3.—Also the occlusal surface of this molar consists of three dentine fields. The buccal salient and reentrant angles are little reduced.

M2.—Four *M2* from sample CM 20416 are assigned to *P. cumberlandensis* on the basis of thick enamel. Three of them are remarkable for having a narrow fold at the anterobuccal side of T3. The shallow posterior folds have no crown cementum.

M3.—Twenty-one *M3*'s from CM 20416 are assigned to *P. cumberlandensis*. Behind the oblique AL follow two broadly confluent, opposing triangles and a short posterior loop (PL), which is provided with two salient angles and usually, two very shallow folds. The PL may bear an additional dentine tract (Fig. 6b).

Remarks on Pitymys McMurthrie 1831

The type species of *Pitymys* is *P. pinetorum* (Le Conte), the North American pine vole. Its dentition shows thick, little-differentiated enamel, more or less rounded salient angles, and rather narrow reentrants. The buccal reentrants of the three-triangled *m1* have aptly been described as "anteriorly oriented half crescents" by Paulson (1961: 148), and are unlike those in *Microtus* *m1*'s in which the posterior part of the buccal reentrants are bent medially. *Microtus* dentitions differ further in having fairly thin well-differentiated enamel, pointed salient angles, and wide reentrants.

The eastern *Pitymys pinetorum* (with subspecies *pinetorum*, *scalopsoides*, and *auricularis*), *P. parvulus* from Florida and the western *P. nemoralis* form a closely related group of species (Fig. 13H–K). The latter two are usually considered as subspecies of *P. pinetorum*. There are, however, consistent dental differences, which a paleontologist would not hesitate to translate in specific separation. In *P. pinetorum* *m3* and *M3* may be a little reduced in size relative to the other elements. In *P. parvulus*, however, the *m3* and *M3* are conspicuously reduced in size, and the *M3* often shows a single dentine field at the occlusal surface, whereas there are three or four in *P. pinetorum* due to the greater depth of the reentrants. *P. nemoralis* is larger than the two other species, the enamel is better differentiated and the connection between anterior cap and T4–T5 in *m1* is narrower. The *M3* and *m3* of *P. nemoralis* are not reduced. The shape of the salient and reentrant angles may be somewhat *Microtus*-like, but the unreduced parts of the enamel are thick as in *P. pinetorum*.

P. cumberlandensis, thus far known from Maryland and Arkansas, is regarded as the ancestor of the three *Pitymys* species mentioned above. Its dentition fits the characteristics of *Pitymys*. It is more primitive than the living representatives in the virtually undifferentiated enamel and in the less elaborate anterior cap. The latter observation is illustrated by the fact that two out of 67 *m1*'s of *P. cumberlandensis*

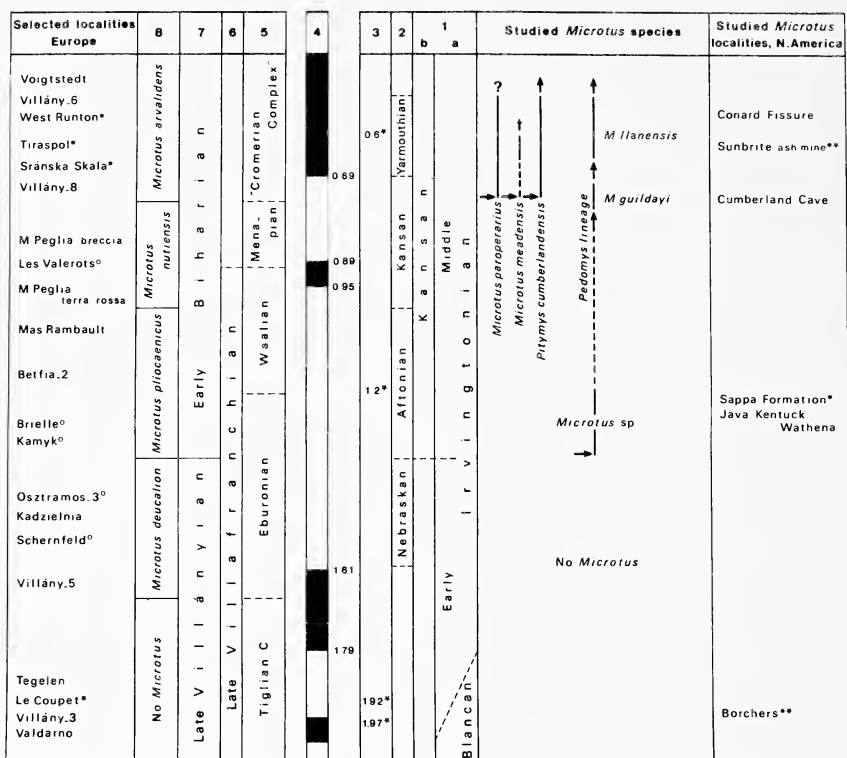


Fig. 14.—Correlation chart between Irvingtonian and Biharian *Microtus* faunas with the aid of absolute and magnetic datings. Absolutely dated localities and paleomagnetically studied localities are indicated with an asterisk and a solid circle, respectively. The absolute dates are given in column 3.

The succession of the studied *Microtus* localities is given in the far right column. The absolutely dated Sappa Formation (with *Microtus*) and Borchers locality (without *Microtus*) are added. The succession of the former localities is based on the steps in the *Pedomys* lineage. Correlation with the Irvingtonian land mammal stage (column 1a) is discussed in the text. Different opinions on the criteria to recognize the Irvingtonian and Blancan (for example, Hibbard, 1972; Zakrzewski, 1975) are expressed by the obliquely drawn boundary between these two stages. Column 1b shows the use of the Kansan Glacial Stage by vertebrate paleontologists (for example, Zakrzewski, 1975). For comparison Berggren and Van Couvering's (1974: Fig. 14) calibration of the North American climatic stages (column 2) with the Standard palaeomagnetic time scale by Cox (1969) (column 4) is given.

The succession of the selected European localities is based on voles and follows from the author's (1975) biozonation (column 8) of the Late Villányian and Early Biharian of the Hungarian Pleistocene subdivision by Kretzoi (1941). An open circle accompanying some localities indicates the presence of lemmings in today's temperate zone of Europe marking cool climate. The evidence for the correlation between the Hungarian and Dutch subdivision (column 5) is discussed in the text. The correlation of the sequence of the latter to the paleomagnetic scale is from Zagwijn (1975: Fig. 8) which in its turn

Table 5.—Measurement and ratio data for ml's of *Pitymys cumberlandensis*, new species, from Cumberland Cave.

Parameter	N	Mean \pm SE	SD	Range
L	45	2.535 \pm 0.023	0.151	2.28–2.87
A/L	45	48.2 \pm 0.36	2.38	44–53
W'/W	42	92.6 \pm 0.63	4.06	84–102
B/W	42	16.2 \pm 0.82	5.30	6–27
C/W	42	15.1 \pm 0.79	5.10	6–32

show cement in the fourth buccal reentrant as opposed to 56 out of 112 in *P. pinetorum* from the Recent sink hole to New Paris 2 (Guilday et al., 1964). This indicates the better development of BRA4 in the living representative, because cement is present only if the reentrant has reached a certain depth.

P. cumberlandensis cannot be derived from a known *Microtus* species, because in its thick enamel, rounded salient angles, and narrow reentrants it is more primitive than even the oldest *Microtus* (*Allophaiomys*).

It is concluded that the *Pitymys* species discussed here form a separate genus of unknown origin with distinct dental characteristics of unknown origin. The genus does not include *Microtus meadensis* from the Cudahy fauna, which have *Microtus* type molars. *M. oaxacensis* has not been seen. *Microtus quasiater* molars resemble those of *M. meadensis*. The separated anterior cap in ml is somewhat less elaborated in the former and a number of variants closely resemble the fossil *M. gregaloides* from Europe. It has been proposed that *M. quasiater* is a disjunct western representative of a cline connected to *P. pinetorum* through *P. nemoralis*. This cannot be disproved on dentitions alone, but seems unlikely. Although intermediate in the degree of separation of the anterior cap, *P. nemoralis* has thick enamel, and the general shape of salient and reentrant angles is quite unlike *P. quasiater*, in which the enamel is thin, the salient angles pointed, and the reentrants wide as in *Microtus*.

This study does not include living "*Pitymys*" from Eurasia. Judging from Chaline's (1972) excellent figures at least some of them (for example *P. duodecimcostatus* and *P. lusitanicus*) may belong to the American genus. Supposedly true *Pitymys* forms appear in France in

←

is mainly based on Van Montfrans (1971). Azzarolli's (1970) correlation of the Late Villafranchian (column 6) with the Dutch sequence is added for reasons of comparison (see text).

Late Middle Pleistocene localities, such as Nestier and Lazaret. The molars determined as *Pitymys subterraneus* from Saint-Estève-Janson (Chaline, 1972) and the Biharian (Middle Pleistocene) *Microtus arvaldens* and *M. gregaloides* do not belong to *Pitymys* in which they have been traditionally placed. Their general dental characteristics are those typical of *Microtus* (*Allophaiomys*) (Chaline, 1972; van der Meulen, 1973).

AGE OF THE CUMBERLAND CAVE FAUNA

The biostratigraphic position of the Cumberland Cave deposits will be based on the arvicolids alone, the evolutionary stages of *Microtus* and *Ondatra* in particular. Presently the following list of the lemming and vole assemblage can be given (after Gidley and Gazin, 1938; Guilday, 1971; Zakrzewski, 1975; and the author's observations): *Synaptomys cooperi* Baird; *S.* (*Mictomys*) sp.; *Ondatra annectens* (Brown); *Atopomys salvelinus* Zakrzewski; *Phenacomys* sp.; *Clethrionomys* cf. *gapperi* (Vigors); *Pitymys cumberlandensis*, new species; *Microtus guildayi*, new species; *M. paroperarius* Hibbard. Guilday (1971) assigned a pre-Wisconsin, supposedly Illinoian age to Cumberland Cave. Recently Zakrzewski (1975: 261) remarked: "If the Cumberland Cave local fauna had been located on the Great Plains, the association of *Ondatra annectens*, *Neofiber*, and *Atopomys*, and the lack of *Microtus pennsylvanicus*, would suggest a pre-Illinoian age." *Neofiber* is not present in Cumberland Cave, as was stated by Guilday (1971).

The study of *Microtus* confirms Zakrzewski's suggestion (Fig. 14). *M. guildayi* is closely related to *M. llanensis* from the Cudahy, Vera and Conard Fissure local faunas from the Great Plains and Ozarks. In all three faunas *Ondatra annectens* and *Microtus paroperarius* are present, whereas *Pitymys cumberlandensis* occurs in Conard Fissure. These distributions point to a close relationship in age of the mentioned localities. Cumberland Cave is thought to be the oldest because *M. guildayi* is somewhat more primitive than *M. llanensis*. The compared localities from the central U.S. have all been assigned to the Kansan Glacial Stage, and to the Irvingtonian Mammal State (for example, Hibbard, 1970; Hibbard and Dalquest, 1966; Graham, 1972) and to the middle part of the Irvingtonian by Zakrzewski (1975).

Other localities in the Midwest assigned to the Kansan and Irvingtonian are Kentuck (Hibbard, 1952; Semken, 1966; Zakrzewski, 1975), Wathena (Einsohn, 1971; Zakrzewski, 1975), type Sappa Formation (Schultz and Martin, 1970), and Java (Martin, 1973). The *Microtus* from these localities are more primitive than *M. guildayi*, and indicate an older age than Cumberland Cave and Cudahy. The latter is generally considered to be Late Kansan. Martin (1973) already considered Java to be older than Cudahy. Dreeszen (1970) considers the Nickerson

Till that overlies the fossiliferous beds at Wathena as Early Kansan. The Type S Pearlette Ash (Coleridge ash) in the type Sappa Formation dates 1.2 m.y., whereas the Type O Pearlette Ash overlying the Cudahy fauna is dated as 0.6 m.y. These dates are in accordance with the biostratigraphical sequence suggested by the *Pedomys* lineage, but are not consistent with correlations in the literature. The fauna from the Sappa Formation is thought to be a Cudahy equivalent by Schultz and Martin (1970) and is placed in the Late Kansan by these authors and Dreeszen (1970).

Study of *Microtus* cf. *llanensis* from the Sappa Formation is, therefore, needed. If it resembles the Wathena *Microtus* (Einsohn, 1971: 65, Pl. 8, Figs. 1–3, 5–8), and is more primitive than the Cudahy *M. llanensis*, it will be difficult to maintain age differences between Wathena and Sappa and age equivalency of Sappa and Cudahy.

There is a further discrepancy between the succession based on *Microtus* and that on *Ondatra* (Semken, 1966; Nelson and Semken, 1970), which shows two trends utilizing length and width of the first lower molar and the height of the first labial dentine tract.

In my opinion the discrepancy arises merely from the independent use of the two parameters in *Ondatra*. Dentine tracts are those vertical areas along salient angles by which high crowned arvicolid molars are attached to the alveolar walls (Mahn, 1890). Their development and increase in height (independent of size increase of the molars) permit the molars to become high crowned and, eventually, unrooted in the course of evolution, as they take over the function of roots. So, although the distributions of length and width of the m1's made by Semken give information only on size, the distribution of dentine tracts reflects a combination of size and hypsodonty. It would, therefore, be worthwhile to compute the length/dentine tract height ratios of *Ondatra* and *Pliopotamys* in order to test the increase of hypsodonty independent from size variations.

All *Ondatra* m1's from Wathena and most of them from Kentuck are larger than the Cudahy m1's and both Semken (1966) and Einsohn (1971) conclude that Cudahy is older than the first two mentioned localities. However, the dentine tracts are of the same height in all three assemblages. This indicates that the Wathena and Kentuck specimens are more primitive, because the relative heights of their dentine tracts are lower than in the Cudahy specimens.

The size of the m1's in living *Ondatra* is variable and shows a definite correlation with latitude; northern populations are larger than more southern ones (Nelson and Semken, 1970). The presence of two size groups of *Ondatra* in Kentuck (and a few other localities) may be explained by assuming glacial-interglacial shifts of biotopes during deposition. In conclusion, the *Ondatra* chronocline does not disprove

the succession resulting from the *Pedomys* lineage, and in fact, it can be easily matched.

The two measurable *Ondatra annectens* m1's from Cumberland Cave (5.1 and 5.3 mm) are a trifle smaller than the Cudahy m1's (5.4–6.0 mm). Dentine tracts could not be measured due to the advanced stage of wear of the Cumberland specimens.

The suggested Middle Irvingtonian age of Cumberland Cave makes the presence of *Synaptomys cooperi*, *Clethrionomys* cf. *gapperi*, *Pitymys*, and *Microtus paroperarius* the oldest North American occurrences of these taxa. *Phenacomys* is present in the Java local fauna (Martin 1973).

Synaptomys (*Mictomys*) sp. from Cumberland Cave differs from the living *S. borealis* in the absence of crown cementum in the posterior buccal reentrant of m3 and in the shapes of the two middle lingual salient angles of m1 (LSA2 and LSA3). In *S. borealis* LSA3 is much narrower than LSA2, whereas the posterior wall of LSA2 (also in m2) is concave. In the Cumberland Cave m1 LSA2 and LSA3 are subequal (LSA3 may be slightly narrower) and the posterior side of LSA2 is convex (also in m2). In these characters *S. (Mictomys)* sp. from Cumberland resembles *S. (Mictomys) kansasensis* from Kentuck, Wathena, and Java and *S. (Mictomys) meltoni* from Cudahy. However, in the latter two species the enamel thickness differentiation is extreme, whereas it is hardly noticeable in Cumberland molars. The living and fossil species are all closely related.

Atopomys salvelinus is slightly more advanced than *A. texensis* from Fyllan Cave, which is accompanied by a *Microtus* species closely resembling *M. guildayi* (Zakrzewski, 1975 and the author's observations). Zakrzewski (1975) thinks that *A. texensis* is not directly ancestral to *A. salvelinus* because the latter has a more simple anterior loop than the former. He is, however, mistaken when he states that a trend towards simpler loops is not yet known among arvicolids. In several lineages of *Mimomys*, for instance, crenulations are lost and islets and ridges are more and more restricted to younger ontogenetic stages (for example, Forsyth Major, 1902; Kretzoi, 1969). This results in more simple patterns in later species. There seems to be no impediment to deriving *A. salvelinus* from *A. texensis* and, for that matter, *Atopomys* from *Nebraskomys*.

Thus far *A. salvelinus* from Cumberland Cave and Trout Cave are the latest known occurrences of the genus.

INTERCONTINENTAL MIGRATIONS OF *MICROTUS* DURING THE MIDDLE IRVINGTONIAN

The comparisons of the Middle Irvingtonian/Kansan *Microtus* with Early Biharian relatives from Europe resulted in the recognition of

three pairs of closely resembling species. These are *Microtus meadensis*-*M. arvalidens*, *M. paroperarius*-*Microtus* sp. C (from, for instance, Villány-8; van der Meulen, 1975), and *Microtus* sp. (from Wathena and Kentuck)-*M. pliocaenicus*.

The similar dental morphologies in these species on both sides of the Bering Strait are definite evidence for the occurrences of migrations. On the basis of the compared species a correlation of Middle Irvingtonian and Early Biharian seems to be suggested. Dental morphology alone, however, does not permit such a conclusion, because of possible and demonstrated differences in rates of evolution in different parts of the Holarctic. For instance, dentitions such as found in *Microtus* (*Allophaiomys*) sp. and *M. (Allophaiomys) pliocaenicus* are restricted to the Irvingtonian in North America and to the earliest part of the Biharian in Europe, but are still present in some living species of *Microtus* (*Phaiomys*) in Asia. To limit the timespan during which the migrations took place one has to look for well-established correlations between the two areas.

In North America there are two absolute dates directly related to *Microtus* bearing sediments (Zakrzewski, 1975). The Coleridge Ash, dated 1.2 m.y. overlies *Microtus* sp. bearing beds in the type section of the Sappa Formation. *M. paroperarius* and *M. meadensis* of the Cudahy local fauna occur in normally magnetized sediments directly underlying the Pearlette Type "O" ash dated 0.6 m.y. This evidence indicates an early Brunhes age of the magnetic time scale (Lindsay et al., 1975). In addition there is the date of ± 2 m.y. for the Early Irvingtonian fauna (without *Microtus*) of Borchers (Hibbard and Dalquest, 1973).

There are no absolute dates for *Microtus* faunas in Europe. Paleomagnetic studies of the Tiraspol section (Nikiforova et al., 1970) in Russia, Stránska Skála in Czechoslovakia (Kukla, 1971), and the Upper Freshwater Bed of the Cromerian type section in East Anglia (Van Montfrans, 1971), indicate that the 0.7 m.y. Matuyama-Brunhes boundary falls in the third, *Microtus arvalidens* Zone (Van der Meulen, 1973 to replace the Nagyarsányhegy and Templomhegy phases of Kretzoi, 1965) of the Biharian. The pre-*Microtus* fauna from Saint Gorges d'Aurac, France, below the Coupet basalt, has been dated as 1.9 m.y. (Chaline and Michaux, 1969). It has been considered that *Microtus* immigrated into Europe at about the beginning of Eburonian, which falls in the Gilsa event, ± 1.6 m.y. (Van Montfrans, 1971; Van der Meulen and Zagwijn, 1974).

The absolute dates and paleomagnetic evidence show that the compared *Microtus* lived during the same time interval. This conclusion greatly increases the significance of the observed morphological similarities of the species in question.

It seems safe to assume that Eurasia was the evolutionary center. Although little is known from Asia, the studies of Chaline (1972) and Van der Meulen (1975) lead to the recognition of gradual changes during the Biharian of Europe starting with the Late Villányian *M. deucalion*, which is the most primitive known representative of the genus. The author (Van der Meulen, 1973) has estimated a very rapid development of *Microtus* during the Villányian-Biharian in Europe. Since that paper was submitted (1972), it became clear that *M. deucalion* is a valid species (Van der Meulen, 1974) and that the Matuyama-Brunhes boundary should be correlated to the *M. arvalidens* Zone of the Biharian (see above). Therefore, it can now be estimated that the development from *M. deucalion* to *M. arvalidens*, *M. gregaloides* and *Microtus* sp. C, each of these three lineages consisting of four recognizable successive steps, took place in ± 1 m.y. It is assumed that the *Microtus* evolution in Asia of which there are only few data available to the author, did not develop more rapidly than in Europe.

Accepting Eurasia as the evolutionary center of *Microtus* during the considered time interval, and the high evolutionary rate of *Microtus* development in Europe as maximal, the dating of *Microtus* species immigrations into North America may be given as maximal ages in terms of European stratigraphy.

Bearing the above data and assumptions in mind, the following conclusions are drawn.

1) The immigration of the Wathena and Kentuck *Microtus* took place during the earliest part (*M. pliocaenicus* Zone, Van der Meulen, 1973 = Betfia phase, Kretzoi, 1965) of the Biharian; probably during the end of Eburonian. In recent literature the immigration of *Microtus* in Europe has been taken as the event marking the beginning of the Biharian (Fejfar, 1976). This is not correct since the earliest *Microtus* (*Allophaiomys*) *deucalion*, is present in Villány-5, which Kretzoi (1956) included in the Villányian on the predominance of *Mimomys*. The author follows Kretzoi and considers *M. (Allophaiomys) pliocaenicus* as marking the beginning of the Biharian. It follows that the immigration of *Microtus* sp. in North America does not predate the European Biharian, unless the *M. deucalion*-*M. pliocaenicus* evolution took place more rapidly in Asia than in Europe, which possibility has been rejected. Because *Microtus* sp. is in some respects slightly more primitive than *M. pliocaenicus* from its type locality, Betfia, which is placed in the middle part of the *M. pliocaenicus* Zone, its immigration is assumed to have taken place during the beginning of the range of *M. pliocaenicus* and, therefore, of the Biharian. The Villányian-Biharian boundary is straddled by the Eburonian, which in the Brielle boring yielded *M. pliocaenicus* (van der Meulen and Zagwijn, 1974). Hence, the conclusion is reached that *Microtus* sp. immigrated during the late

part of the Eburonian. The date of 1.2 m.y. for the *Microtus* sp. bearing fauna in the Sappa Formation is not inconsistent with an Early Biharian/Late Eburonian immigration.

2) The immigration of *M. paroperarius* and *M. meadensis* took place during the early part of the *M. arvalidens* Zone (third and latest zone of the Early Biharian in Van der Meulen, 1973). *Microtus* sp. C and *M. arvalidens* appear simultaneously in the older localities (for instance, Villány-8) of the *Microtus arvalidens* Zone of the Biharian. They descend from *M. burgondiae* (= *M. (Allophaiomys)* sp. B in Van der Meulen, 1973) and *M. nutiensis* (= *M. (Allophaiomys)* sp. A in Van der Meulen, 1973) from the preceding Zone. It is premature to speculate whether the absence of *M. meadensis* in Cumberland Cave indicates that *M. paroperarius* immigrated before *M. meadensis* did, considering the few data at hand. The absolute and paleomagnetic dates show that the immigration of the two American species followed very shortly their origin in Eurasia.

The two migrations into North America took place just prior to 1.2 m.y. and ± 0.7 m.y. ago. The timespan embraced is represented by Lower Biharian sediments in Europe and Middle Irvingtonian sediments in North America. Berggren and Van Couvering (1974) think that the Biharian follows the Villafranchian. In the author's opinion, the earliest part of the Biharian and Late Villafranchian are time equivalent. In European Russian localities (Kair and Nogaïsk) and western Siberian sections (Kizikhan and Razdolian) Early Biharian arvicolids, *Microtus (Allophaiomys)* and *Prolagurus*, occur together with Late Villafranchian indicators such as *Elephas meridionalis* (see Kretzoi, 1965; Vangenheim and Zazhigin, 1972). The absence of such co-occurrences in western European localities seems to be a result of the assemblages consisting of small or large mammals. In an as yet unpublished fauna from southern Italy collected by Dr. M. Freudenthal, *Microtus pliocaenicus* and *Equus stenonis* are present. Other evidence contradicting Berggren and Van Couvering's estimate of 0.9 m.y. for the base of the Biharian is the evolution of *Microtus*, which would require more than the some 200,000 years permitted from their scheme.

The scarce finds of arvicolids in dated Dutch sections are all consistent with the biozonation given in Van der Meulen (1973). Presently these finds are *Microtus pliocaenicus* in the Eburonian (Van der Meulen and Zagwijn, 1974), *M. burgondiae* in the Menapian (Van der Meulen, 1973), and the unpublished find of *M. gregaloides* in Glacial A or Interglacial II sediments of the "Cromerian Complex," placed near the Brunhes-Matuyama boundary (Zagwijn et al., 1971). Thus, a correlation between Early Biharian and the Late Eburonian-"Cromerian" of the Dutch scale and Late Villafranchian-Cromerian of the traditional European scale seems likely.

Lindsay et al. (1975) concluded that the Blancan-Irvingtonian boundary falls in the early part of the Matuyama below the Olduvai event of 1.86–1.71 m.y. Faunistic changes by which they recognize the boundary are the extinction of *Hypolagus*, *Borophagus*, and *Nannipus* and the appearance of *Lepus*, *Dipodomys*, and *Ondatra*. Hibbard and Dalquest (1973) place the Borchers fauna, dated 1.97 m.y., in the Irvingtonian utilizing the same faunal criteria. Apparently the major change in the arvicolid fauna was yet to come. The few vole species in the Borchers fauna are the same as in typical Late Blanchan faunal assemblages from Grand View and White Rock (Eshelmann, 1975). The change in the arvicolids is characterized by the extinction of Blancan forms (for example, *Ophiomys*) and the appearance of *Microtus*, which becomes the dominant vole. A similar change (rise to dominance of *Microtus*, extinction of many *Mimomys* species) characterizes the Villányian-Biharian boundary in Europe. It seems from our dating of immigration of *Microtus* sp. and the few absolute dates of the Early Irvingtonian and Late Villányian that the change took place at roughly the same time in Europe and North America.

COMPARISON OF MIDDLE PLEISTOCENE *MICROTUS* EVOLUTION IN EUROPE AND NORTH AMERICA

The comparison is restricted to the Late Villányian-Early Biharian *Microtus* from Europe and their Middle Irvingtonian relatives in North America. Data for the Asian development are insufficient for comment.

The evolution of European *Microtus* has recently been studied in detail by Chaline (1972) and Van der Meulen (1973). In this section only the pattern arrived at by the author is considered for reasons explained in the next section.

Although Chaline and the author differ considerably on several aspects of *Microtus* dental evolution, they agree on the existence of the main trends, which consists of complication of the anteroconid complex of m1 in two different ways. Starting with a three-triangled m1 pattern with simple anterior loop characteristic of the subgenus *Allophaiomys*, one lineage leads to the "Pitymys" pattern in which the anteroconid complex is divided in two fields consisting of T4-T5 and AC2. In the other, *Microtus*, lineage T4 and T5 and eventually AC2 are separated (Fig. 15). This evolution started with *Microtus deucalion*, which immigrated to Europe during the Late Villányian (± 1.6 m.y.). Toward the end of the Early Biharian, approximately 1 m.y. later, at least four descendants were present—*M. arvalidens* and *M. gregaloides* of the "Pitymys" lineage and *Microtus* sp. C and *Microtus* sp. D (with different percentages of Hinton's 1926, *M. ratticepoides*, *M. nivaloides*, *M. nivalinus*, and *M. arvalinus* morphotypes) of the *Microtus* lineage.

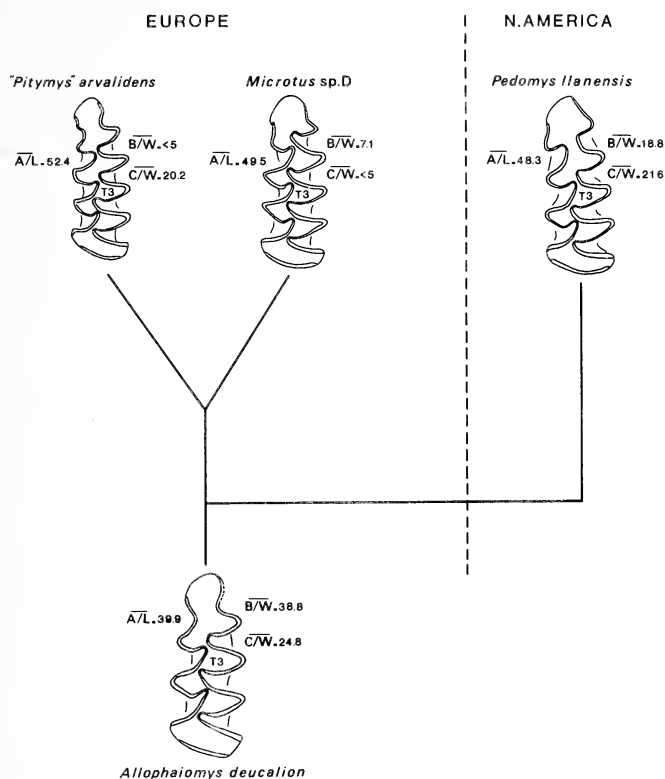


Fig. 15.—Simplified evolutionary scheme of early *Microtus* m1 in Europe and North America illustrating the different ways of complication of the anteroconid complex, which is the part in front of the third triangle, T3. The means of the ratios of the European species are from Van der Meulen (1973, 1974). *M.* ("Pitymys") *arvalidens* and *Microtus* sp. D are the most advanced Biharian species of the "Pitymys" and *Microtus* lineage, respectively. They are thought to be approximately contemporaneous with *M.* (*Pedomys*) *ilanensis*. *M.* (*Allophaiomys*) *deucalion* is the oldest known *Microtus* species.

The relationships of the *Microtus* species to different biotopes has been discussed (Van der Meulen, 1973) from their differing frequencies in several small assemblages. The study led to the recognition of three main factors involved in the rapid, branching evolution—a) the main trends are adaptive, b) the high rate of production, and c) climatic changes in the distribution area of the species forcing the populations to adapt or to migrate. Migration probably increased isolation of population groups each of which probably adapted to respective local environments.

No such rapid and diversified evolution seems to have taken place in North America during the Middle Irvingtonian, but it is realized that data are largely restricted to the Great Plains. As outlined before *Microtus* immigrated to North America somewhat more than 1.2 m.y. ago. This earliest species, *Microtus* sp. from Kentuck and Wathena, gave rise to *M. llanensis* (± 0.6 m.y.) through *M. guildayi* in what is called the *Pedomys* lineage. The other two Middle Irvingtonian species, *M. paroperarius* and *M. meadensis*, are considered immigrants, because no intermediate species between these and *Microtus* sp. are known. It was also argued that *Pitymys cumberlandensis* (probably immigrating together with *Microtus paroperarius* and *M. meadensis*) and its living representatives form a separate group not to be included in *Microtus*. *M. deceitensis* from Alaska can be derived from any primitive *Microtus* species with a three-triangled m1 and a simple anterior loop, for example *M. pliocaenicus* or the Kentuck and Wathena *Microtus*. The partial separation of the middle triangles in m3, the asymmetrical anteroconid complex in which the buccal features are better developed than the lingual ones, and the combination of four-triangled m1 and two-triangled M3 do not allow *M. deceitensis* to be fitted into the known *Microtus* trends. The first two characters bar it from being ancestral to *M. paroperarius*. Thus, *M. deceitensis* is considered to represent a separate *Microtus* lineage, possibly leading to *M. xanthognathus* with which it shares the m3 morphology (John Guilday, personal communication), and the asymmetrical anteroconid complex.

The *Pedomys* lineage is represented today by *Microtus* (*Pedomys*) *ochrogaster*. The overall change in m1 morphology is comparatively small in the *Pedomys* lineage because the m1 in the living *Microtus ochrogaster* are still three-triangled and more primitive than in any European species living 700,000 years ago. Another characteristic of the *Pedomys* lineage is the probable absence of side branches, whereas in Europe both *Microtus* and "*Pitymys*" lineages are each represented by two species in the late part of the Early Biharian. It seems that populations of *Pedomys* were not isolated long enough (if at all) for local adaptations to occur, in spite of the climatically forced migrations, which one may expect to have happened. The absence of major east-west barriers in the Great Plains, where *Pedomys* lives today, may explain the straight line development.

The European "*Pitymys*" and *Microtus* lineages and the *Pedomys* lineage seem to constitute a case history of parallel dental evolution. In each lineage, complication of the anteroconid complex takes place by enlarging existing and adding new salient and reentrant angles. This overall trend is reflected by the increase of the mean of A/L values standing for the relative length of the anteroconid complex (Fig. 15) in all three lineages. In the "*Pitymys*" and *Pedomys* lineage the mean

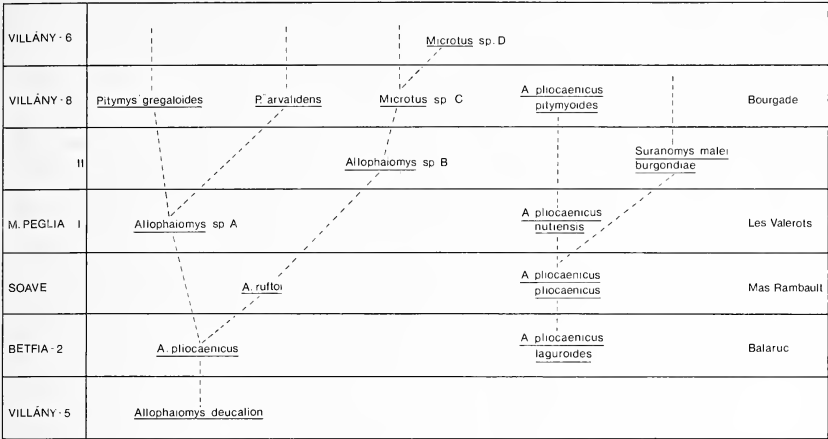


Fig. 16.—Comparison of the different determinations and resulting evolutionary relationships of early European *Microtus* species by Chaline (1972) at the right, and by Van der Meulen (1973) at the left. The localities that yielded the ml's on which the two schemes are based, are given. A taxon (or taxa) from the one scheme refers to the same morphologies as the taxon (or taxa) from the other scheme placed at the same level. *Microtus* (*Allophaiomys*) *ruffoi* is considered as a valid taxon by the author only.

of C/W (communication between T4 and T5) changes little, but in the former the mean of B/W (communication between AC2 and T4-T5) becomes much lower than in the latter. The *Microtus* lineage is primarily characterized by the decrease of the mean of C/W; in *Microtus* sp. D from Villány-6 the mean of B/W is also low, but not in *Microtus* sp. C and *M. paroperarius* of the same lineage.

COMMENTS ON CHALINE'S MODEL OF EARLY BIHARIAN
MICROTUS EVOLUTION

The evolution of *Microtus* is a subject of potential interest not only to the specialists of voles, but also to other students of evolution. The author is convinced that it is possible to reconstruct, step by step, a "family tree" of *Microtus* (and other vole genera as well) on a more refined scale than is possible for many other animal groups.

It is, therefore, confusing that Chaline (1972, 1974) and the author have developed quite different evolutionary patterns and interpretations of Early Biharian *Microtus* evolution in W. Europe. A preprint of Chaline's thesis was kindly made available in 1972 to the author before his thesis was in print, but too late to include an extensive discussion on it. Since then Chaline (1974) has further expanded his concepts on *Microtus* evolution to include all Holarctic species. Chaline and Michaux (1975) also have described a new example of vole

cladogenesis resulting from sympatric evolution following the same approach as in Chaline (1972). Only the Early Biharian part of the *Microtus* evolution will be discussed in this paper (Fig. 16).

On the basis of the material from the localities Balaruc, Mas Rambault, Les Valerots, and Bourgade, Chaline constructs his *Microtus* (*Allophaiomys*) *pliocaenicus* lineage as a series of successional subspecies—*laguroides*, *pliocaenicus*, *nutiensis*, and *pitymyoides*. In Les Valerots the subspecies *nutiensis* is accompanied by *Microtus* (*Suranomys*) *malei burgondiae*. These two forms are considered as two species *in statu nascendi*, representing an early phase of the branching off of the *Suranomys* lineage. Chaline hypothesizes that it is the result of sympatric speciation.

Fig. 16 shows the taxonomic nomenclature used by Chaline and the author. The following discussion attempts to show that the different evolutionary patterns follow from different interpretations of the variation in m1 morphology and from different methods in determination. Additionally there are different opinions on the validity of taxonomic names and on the type of classification to be followed—more vertical by Chaline and more horizontal by the author.

Microtus (*Suranomys*) Chaline 1972 is considered here to be the junior synonym of *M.* (*Chionomys*) Miller 1908, because it includes *M. nivalis*, which is the type species of the latter. It is possible that *Microtus* sp. C and D belong to *Chionomys* (van der Meulen, 1975: 100–101). Assigning *burgondiae* to the subgenus *Chionomys* or to *Allophaiomys* depends on the preference for the type of classification mentioned above. The same goes for the use of *M.* ("Pitymys") or *M.* (*Allophaiomys*) for the youngest forms of Chaline's *pliocaenicus* lineage (the author's "Pitymys" lineage).

Chaline's subspecies *laguroides* and *pliocaenicus* are based on *Allophaiomys laguroides* and *A. pliocaenicus* from Betfia, Roumania (Kormos, 1933). *A. laguroides* has been placed in the synonymy of *Microtus* (*Allophaiomys*) *pliocaenicus*, since Kormos' species could not be separated in topotype material (Van der Meulen, 1973). The Balaruc *laguroides*, I think, belongs to *M. pliocaenicus* from Betfia, despite the small size of the former. Judging from Chaline (1972: Fig. 20), *pliocaenicus* from Mas Rambault seems more advanced than the type material of *M. pliocaenicus*, and may be identical to *M. ruffoi* (Pasa, 1947), which Chaline synonymized with *M. pliocaenicus*. The present author regards this synonymy as doubtful.

In Les Valerots the same two species are present as in M. Peglia. They are both closely related to their common ancestor, *M. pliocaenicus* from Betfia. It has been shown that the author's *Microtus* sp. B is more similar to *M. pliocaenicus* than *Microtus* sp. A is (see mean A/L and mean B/W of the three species in Van der Meulen, 1973: Table 4).

It is proposed that the Les Valerots and *M. Peglia* taxa be named *Microtus* (*Allophaiomys*) *nutiensis* = *M. (Allophaiomys)* sp. A and *M. (Allophaiomys)* *burgondiae* = *M. (Allophaiomys)* sp. B, because it seems that vertical classification is carried too far if *nutiensis* is regarded as a subspecies of *pliocaenicus* while *burgondiae* is placed in another species and subgenus.

The separation and, hence, the characterization of the two taxa from Les Valerots as given by Chaline is considered unsatisfactory. The means and ranges of their m1 lengths are obtained from two artificial distributions which resulted from the arbitrarily cutting of the bimodal distribution for the total sample at one of the class boundaries. Furthermore, one of the histograms (Chaline, 1972: Fig. 27a), which is given to show the different morphology of the two size groups, is uninformative because the distribution is homogeneous and the various morphotypes are not indicated. In *M. Peglia* *M. nutiensis* and *M. burgondiae* occur separately in two different strata. The diagnoses based on these assemblages may, therefore, be more reliable than the original ones.

In the following quotation Chaline summarizes his arguments for the sympatric speciation of *M. nutiensis* and *M. burgondiae*. Discussing their m1 morphology he states (Chaline, 1974: 443–444): "L'existence de types morphologiques intermédiaires entre les deux groupes démontre que l'interfécondité devait être encore possible (au moins par la production de F1). Cette structure de population étant assez générale dans toute l'Europe pose la problème du déterminisme de cette cladogenèse qui ne semble pas s'expliquer par un isolement géographique. C'est pourquoi, j'ai proposé à titre d'hypothèse de travail, un processus éventuel de spéciation sympatrique où le facteur d'isolement intraspécifique pourrait correspondre à une modification de l'arrangement chromosomique favorisant les homozygotes. Les observations de R. Matthey (1964) sur les *Leggadas* montrent que ce schéma n'a rien d'in vraisemblable."

The variations in dental morphology of many living *Microtus* show overlap of each other. This is easily explained by their close phylogenetic relationships, and does not necessarily imply cross breeding. Therefore, Chaline's conclusions, that *nutiensis* and *burgondiae* are two species *in statu nascendi* seems speculative. The discussed species are known with certainty from Les Valerots and *M. Peglia* only. Judging from the literature, they may occur in three or four other localities (Van der Meulen, 1973). So the above stated rather general co-occurrence in Europe is true for a small number of localities, but not for *M. Peglia*. Here they occur separately (in as much one can be certain, working with highly variable m1 morphologies) in the lower terra rossa and in the upper breccia. These beds produced quite different small mammal associations. Consequently, *M. nutiensis* and *M. burgondiae* were as-

sumed to have had different habitat preferences. Their succession in M. Peglia was explained by migrations caused by climatic change. In Les Valerots the taxa are found together in the same layers, but even then one must be careful in interpreting this fossil co-occurrence in terms of sympatry. This is shown, for instance, in the carefully sampled bed 12 of Villány 8 (Kretzoi, 1956; Van der Meulen, 1973). Conspicuous changes in the vertical distributions of species, indicating shifts of biotopes, appeared to be present in this single layer (thickness ca. 50 cm).

In the opinion of the author these observations show that Chaline has not produced conclusive evidence opposing the conventional evolutionary reconstruction involving isolation (previous section), and substantiating his attractive hypothesis of sympatric speciation.

Chaline's subspecies *pitymyoides* from Bourgade comprises hintonid/gregalid, arvalid morphotype 3, and ratticepoid morphotype 2 first lower molars, corresponding to the present author's *Microtus gregaloides*, *M. arvalidens*, and *Microtus* sp. C, respectively. The supposed homogeneity of *pitymyoides* has been based on the unimodal distribution of the m1 lengths (Chaline, 1972: Fig. 28), and on the presence of intermediates between most variants. Chaline notes that the ratticepoid molars are not connected by intermediates with the morphotype 3 molars. The present author found the same to be true in the assemblages from Nagyharsányhegy-4 and Villány-8, hence his separation of *Microtus* sp. C. Both in Villány-6 and Nagyharsányhegy-4 hintonid/gregalid (*M. gregaloides*) and arvalid molars (*M. arvalidens*) were separable on measurements of the characteristic anterior dentine field lying in front of the confluent pair of the fourth and fifth triangle typical of morphotype 3 (Van der Meulen, 1975: Fig. 31). The differences between the species recognized by the author are comparable to those between the living *M. arvalis*, *M. gregalis*, and *M. oeconomus*. Different habitat preferences of the fossil species are indicated in vole diagrams (Kretzoi, 1956; Fejfar, 1961; Van der Meulen, 1975). It follows that quantitative analysis of m1 length alone is considered insufficient to evidence the homogeneity of *pitymyoides*.

CONCLUSIONS

1. *Microtus* species, *M. guildayi*, new species, and *M. paroperarius*, and one *Pitymys* species, *P. cumberlandensis*, new species, are identified in the Cumberland Cave fauna.
2. *Pitymys* is considered as a genus, that does not include "*Pitymys*" *arvalidens* and "*P.*" *gregaloides* from the Middle Pleistocene of Europe. *Pitymys cumberlandensis*, the oldest known representative, does not descend from *Microtus* (*Allophaiomys*), which is the ancestral stock of *Microtus*.
3. *Microtus* (*Pedomys*) comprises three North American species only—

- the fossil *M. guildayi* and *M. llanensis*, and living *M. ochrogaster*. These species from a single evolutionary lineage descending from the unnamed *M. (Allophaiomys)* from Wathena, Kentuck, and Java, and probably the type section of the Sappa Formation. The latter *Microtus* is the oldest representative of the genus in North America.
4. The dental evolution in *Pedomys* is parallel to, but slower than, that in the European "*Pitymys*" and *Microtus* lineages.
 5. The age of the Cumberland Cave fauna is Middle Irvingtonian *sensu* Zakrzewski (1975).
 6. Two different migrations of *Microtus* from Eurasia into North America are distinguished. The earlier is the immigration of the Wathena and Kentuck *Microtus* at about the beginning of the Biharian, probably during the Eburonian glaciation, just prior to 1.2 million years ago. The immigration of *Microtus paroperarius*, *M. meadensis*, and *Pitymys cumberlandensis* took place just prior to 0.7 million years, at the beginning of the third, *Microtus arvalidens*, zone of the Biharian.
 7. The Middle Irvingtonian is correlated to the Early Biharian.

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ARTICLE 7

COMPARISON OF THE VASCULAR FLORAL ANATOMY OF *XEROPHYLLUM ASPHODELOIDES* (L.) NUTT. AND *X. TENAX* (PURSH) NUTT. (LILIACEAE-MELANTHIOIDEAE)

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ABSTRACT

The patterns of floral vascularization in *Xerophyllum tenax* and *X. asphodeloides* (Liliaceae-Melanthioideae) are presented and compared. Both species share a three-bundled (lower), a six-bundled (middle), and a 12-bundled (upper) pedicel vascular configuration. The upper configuration consists of six outer, smaller bundles which alternate with six inner, larger bundles. The six smaller bundles are fusion products formed at lower pedicel levels and directly supply the two whorls of tepals. Each tepal-supplying bundle divides to form a median and two laterals. There is further subdivision of the laterals within the freed tepals.

The six larger remaining bundles undergo repeated radial divisions and fusions to form the two whorls of stamen traces. The outer stamen traces are formed in a similar manner as the inner stamen traces. Both are fusion products and their formation closes the gaps left by the departing tepal supply bundles. Axial continuations of these six larger bundles undergo one final radial division to form the fusion dorsals and the free ventrals. The ventrals have a reversed arrangement of their conducting elements. Septal axials, dorsal laterals, and ventral laterals do not occur in either species. *Xerophyllum asphodeloides* has two basal ovules and two associated funicular traces per locule, whereas *X. tenax* has four ovules and four funicular traces arranged in two tiers per locule. The vascularization of the former represents a simplified version of the latter.

The gynoecium in both species is tricarpellate and unilocular with three free styles. Dorsal notches are present, as well as deep septal indentations. Rhaphides occur in both species, but their abundance increases with maturity. The capsule fruit in both species dehisces loculicidally. *Xerophyllum tenax* has a papilloid carpellary epidermis which *X. asphodeloides* does not. Both species have an internal stigmatoidal support system for pollen tube growth which lines the inner styles and the axial faces of the inner septal wing margins.

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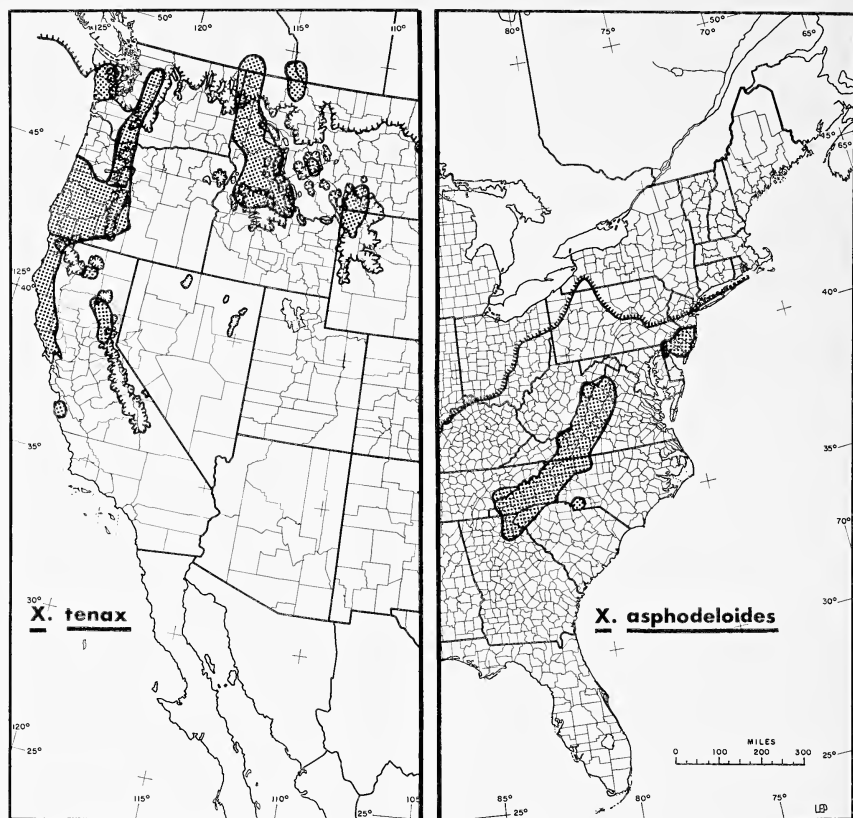


Fig. 1.—Distribution of *Xerophyllum tenax* ("Bear grass;" "Squaw grass") and *X. asphodeloides* ("Turkey beard") in western and eastern North America. Ranges based in part on Wood (1972) and Johnson (1969); glacial boundaries from Flint (1971).

INTRODUCTION

The two species of *Xerophyllum* (Rich.) Michx. are endemic to North America. One species, *X. tenax* (Pursh) Nutt. (= *Helonias tenax* Pursh; = *Xerophyllum douglasi* S. Wats.), is confined to the west, whereas the other, *X. asphodeloides* (L.) Nutt. (= *Helonias asphodeloides* L.; = *Xerophyllum setifolium* Michx.), is limited to the east (Fig. 1). Neither species has had extensive range expansion via migration or dispersal across the Pleistocene continental glacial maxima (Fig. 1; Wood, 1972; Flint, 1971; Johnson, 1969; Maule, 1959). Localized elevational shifts have no doubt occurred in both species. *Xerophyllum tenax* has a broader ecological tolerance than *X. asphodeloides*, as well as a morphological variability, which defies geographical delimi-

tation (Hitchcock et al., 1969). Several chromosome counts are available for *Xerophyllum*—*X. tenax*, $2n = 30$ (Taylor and Brockman, 1966; Cave, 1970), and *X. asphodeloides*, $2n = 30$ (Miller, 1930).

As a primitive lily genus, *Xerophyllum* is distinctive. The tribal association of *Xerophyllum* differs between the Englerian and Hutchinsonian systems. In the former system (Engler, 1888; Krause, 1930), *Xerophyllum* is placed in the tribe Helonieae along with *Helonias*, *Chamaelirium*, *Chionographis*, *Heloniopsis*, and *Metanarthecium*.

Hutchinson (1934), on the other hand, divides these genera and adds others in the formation of two different tribes—Heloniadeae (emend.) with *Helonias*, *Chamaelirium*, *Ypsilandra*, and *Chionographis*, and Nartheciae with *Pleea*, *Tofieldia*, *Hewardia*, *Heloniopsis*, *Clara*, *Narthecium*, *Metanarthecium*, *Aletris*, and *Nietneria*. *Xerophyllum* is placed in the latter tribe (Hutchinson, 1934).

It is hoped that this detailed comparison of the floral vascular anatomy of both *X. tenax* and *X. asphodeloides* can be used as a floral benchmark in future tribal delineation.

MATERIALS AND METHODS

Materials for this study were collected over a two year period. Both flowering and fruiting materials were collected. Buds through fruits were fixed in 3:1 (absolute ethanol:glacial acetic acid) and stored in 70% ethanol. Living plants are currently in cultivation in Pittsburgh. Voucher specimens have been prepared for both species—*Xerophyllum asphodeloides* (New Jersey: Burlington Co., Mt. Misery, Utech 76-412 CM), and *X. tenax* (Oregon: Clackamas Co., Mt. Hood, Utech 77-401 CM).

Twenty-five flowers (buds to maturing fruits) were sectioned between 12 to 16 μ using standard paraffin techniques and stained in safranin and methylene blue (Sass, 1958; Johansen, 1940). Checks on these serial preparations were made by observing whole flowers that had been both cleared in 10% NaOH and stained in 1% fuchsin (Fuchs, 1963; Utech and Kawano, 1976).

Neither ontogenetic nor teleological implications are intended by the method of vascular description, which traces the hypothetical ascent of the various bundles from the pedicel to the stigmas. In Fig. 3, a series of cross-sections from the lower pedicel (Fig. 3A) to the upper, freed styles (Fig. 3M) is presented for *X. tenax*. These same cross-sections have been projected and redrawn for Fig. 4, such that selected vascular bundles can be followed through the various sections. A scale indicates the approximate level of the various lettered cross-sections. The final summary diagram (Fig. 9) presents the floral vascularization of *X. tenax* as a cylinder which has been opened longitudinally. This type of "roll-out" diagram has been previously used for other liliaceous species (Utech and Kawano, 1975, 1976a, 1976b). Text introduced codes for the various bundles are presented.

OBSERVATIONS

Both species have a many-flowered, simple, terminal raceme. *Xerophyllum tenax* is usually more robust and taller than *X. asphodeloides*, (0.8) –1.2–1.8– (2.0) dm as compared to (4.5) –0.8–1.0– (1.5) dm. *Xerophyllum tenax* also has approximately twice the number of flowers as *X. asphodeloides* (Fig. 2). The lower flowers of both

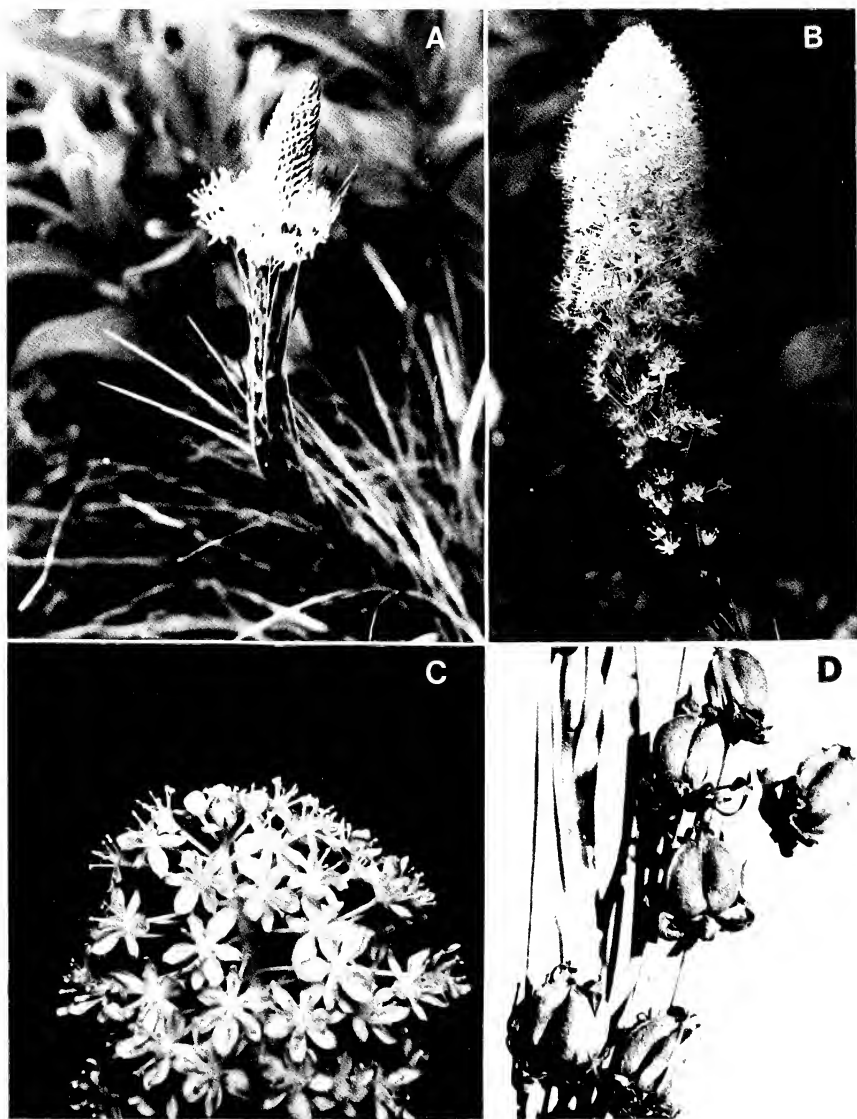


Fig. 2.—Floral comparison in *Xerophyllum*. A) *X. tenax*, spiral bud arrangement in early anthesis also showing transitional setaceous leaves below flowers ($\frac{1}{4}\times$). B) *X. tenax*, elongated floral raceme at midanthesis, pedicels divergent in the upper half and erect in the lower half ($\frac{1}{5}\times$). C) *X. asphodeloides*, flowering portion of terminal raceme showing divergent pedicels ($2\frac{1}{2}\times$). D) *X. asphodeloides*, loculicidally dehiscent capsules with two erect seeds per locule, fruiting pedicels nearly vertical ($3\frac{1}{2}\times$).

species are bracteate, although the upper ones may have only a reduced bract or one adnate to the pedicel for much of its length. The latter is common in *X. asphodeloides*, especially in the early stages of flowering (Fig. 8A–B). Initially the inflorescence appears corymb-like (Fig. 2A–C), but with maturity the raceme axis is elongated. In *X. asphodeloides*, the flowering portion of the axis is between 1.5 and 3.0 dm long, whereas in *X. tenax*, this same region spans 5.0 to 7.5 dm.

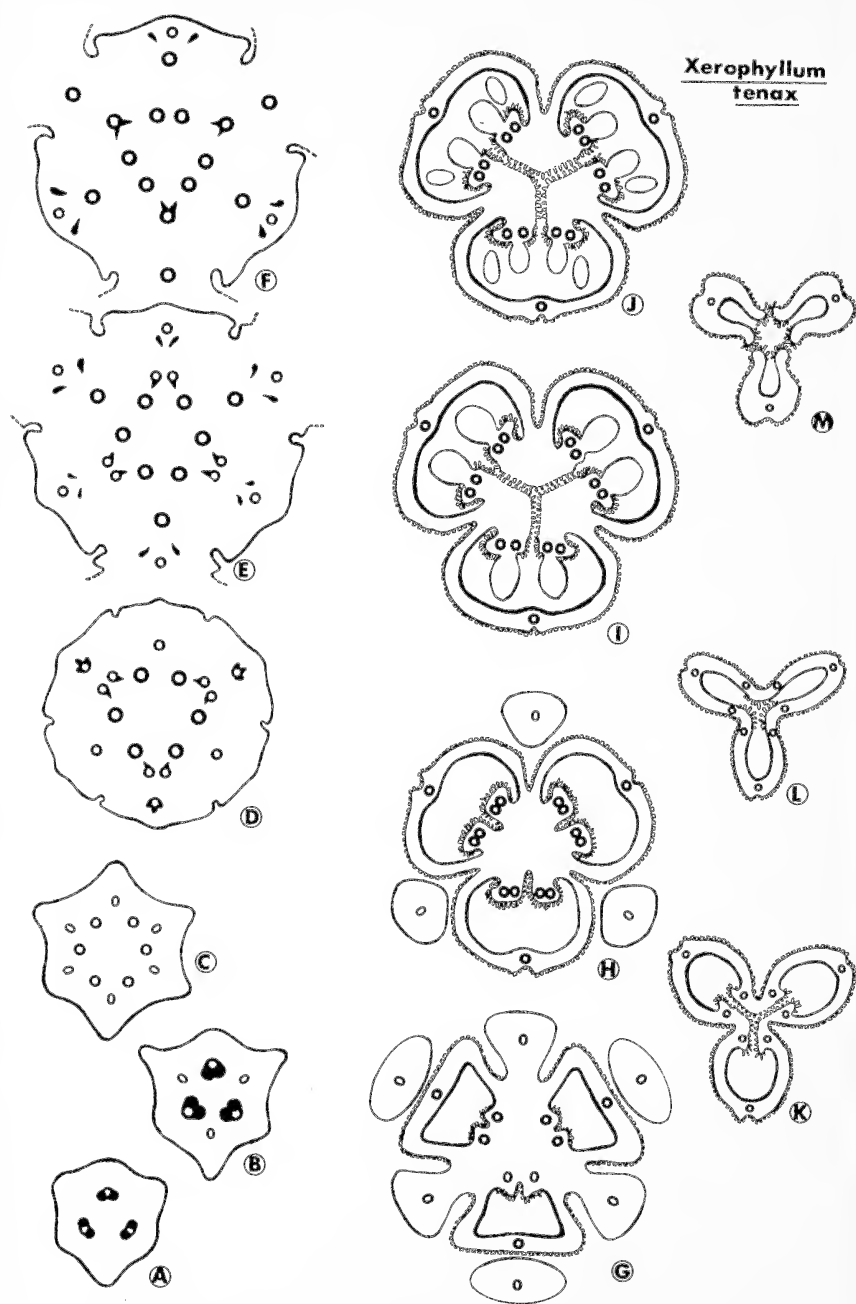
Pedicels and Their Vascularization

Along the flowering raceme of both species, there is a size gradient in the length of pedicel. However, a consistent pedicel length difference does occur between the two species. From our sampled populations, 50 fruiting pedicels of both species were measured for comparison. In *X. asphodeloides*, the mature pedicel averaged 3.32 cm long (range: 2.11–4.56 cm; SD = 0.14), which is significantly shorter than the average pedicel length of 5.31 cm (ranges: 3.95–6.35 cm; SD = 0.55) for *X. tenax*.

The pedicels in both species of *Xerophyllum* have a similar pattern of vascularization, which can be divided into three distinct parts (Figs. 3A–C, 4A–C, 5A–B, 9). The upper portion of the pedicel is characterized by a 12-bundled configuration (Figs. 3C, 4C, 5A–B). These 12 bundles can be further subdivided into two groups. There are six small outer bundles, which alternate with six large inner bundles (Fig. 5B). The 12-bundled pedicel was the beginning point for Anderson's (1940) brief vascular description of *X. asphodeloides*. Further sectioning towards the base of the pedicel reveals additional patterns (Figs. 3, 4, 9) in both species.

Near the midpedicel zone, there is a six-bundled pedicel configuration (Figs. 3B, 4B, 9). Three of these six bundles are continuous with three of the smaller bundles observed at a higher level. These three common bundles are 120° apart and directly determine the outer tepal supply. The outer three bundles in the midpedicel zone are relatively large and crescent-shaped, and the new bundles arise from them. Each crescent-shaped bundle undergoes a division and partial gap-closing fusion in a short vertical distance. Two new bundles result from the division of each of the large bundles. A gap is also created by this type of radial division. Lateral branches from the new bundle pairs are formed almost immediately. These paired lateral branches fuse and close the gap from the division (Figs. 3–4, 9).

The three gap-closing bundles are small, fusion products that are continuous with the three outer smaller pedicel bundles at a higher level. These three bundles directly establish the inner tepal supply. The three gap-closing bundles are 120° apart and each is 60° from another smaller



outer bundle (Fig. 5A). The change from a six- to a 12-bundled pedicel configuration is due to the radial division products (Figs. 3–4, 9).

Near the junction of the pedicel with the inflorescence axis, there is another type of pedicel-bundle configuration. At this basal level, there are only three large crescent-shaped bundles (Fig. 3A, 4A, 9). These three bundles arise directly from the inflorescence axial supply. The three-bundled condition occurs for only a short vertical distance before it also undergoes a division. Each of the three bundles divides radially with a gap created between the product halves. This gap is quickly closed via fusing lateral branches from the product halves (Figs. 3A, 4A, 9). The three fusion products are continuous with the crescent-shaped bundles (three) that underwent a similar type of division at the midpedicel level. The remaining product halves of the lower division fuse in the opposite direction with bundles of similar origin (Fig. 9). These fusion products are 120° apart and establish the three smaller bundles in outer pedicel, which in turn establishes the outer tepal supply.

Within the pedicels of both species, considerable division and fusion occur in the formation of the 12-bundled pedicel configuration from the three-bundled and the 12-bundled configuration of the lower zones. The 12-bundled configuration is essentially a six smaller plus six larger bundled arrangement. The six smaller, outer bundles are all fusion products that establish in two vertically separated whorls the tepal vascularization. The six larger, inner bundles, which alternate with the

←

Fig. 3.—Serial cross-sections of *X. tenax*. A) Lower pedicel with three-bundled configuration. B) Midpedicel with six-bundled configuration. C) Upper pedicel with 12-bundled configuration, that is, six smaller outer and six larger inner. D) Receptacle base, departure of outer tepal supplying bundles, lateral branch pairs forming outer stamen traces. E) Receptacle base, outer and inner tepal supplying bundles dividing to form a median and two laterals, outer stamen traces established, lateral branch pairs about to fuse along septal radii to form the fusion inner stamen traces, six bundles remaining centrally. F) Upper receptacle base, outer and inner stamen traces established, formation of the fusion dorsals, outer tepals cut off, six bundles remaining centrally. G) Gynoecium base with freed outer stamens, dorsals positioned, inner stamen attached along septal radii, paired (three) ventrals centrally, carpellary epidermis with papillae, obturators with papillae. H) Gynoecium with inner stamens freed, dorsal notches present, solid central gynoecium base. I) Mid-gynoecium with central base divided, parietal placentation, unilocular condition, radial division of ventrals (reversed conducting elements), septal indentations evident. J) Mid-gynoecium with second tier of ovules. K) Upper gynoecium and transition to styles, ventral continuations still present. L) Lower common styles with unilocular cavity, septal margin with stigmatoid papillae on margin tips. (See Fig. 4 for transformational projects and a partial interconnection of the various traces and bundles.)

six smaller outer bundles, establish via continued division and fusion the stamen and synoecial supply (Figs. 3A–C, 4A–C, 5A–B, 9).

Were the complete vasculature of the pedicel not observed, one might conclude that the six outer smaller bundles were established as simple nonfusion bundles within the inflorescence axis and that there was no interconnection between the tepal supplying bundles and those, which supply the stamens and carpels (Fig. 9). On the other hand, the total floral vascularization of the upper pedicel can be traced to three large and, indeed, compound bundles. Furthermore, the tepal supply has its origins within the pedicel and not at some planar level within the receptacle.

Tepals and Their Vascularization

The persistent tepals of both species are dull to creamy-white in flower. The three tepals of both the inner and outer cycle are free and distinct, oblong to ovate in shape and without basal glands (nectaries) or claws. Neither species has a readily detectable odor. The tepals of *X. tenax* tend, on the average, to be longer and wider than those of *X. asphodeloides*. The perianth bud bases of both species have an apparent one-sided asymmetry (semirostate), which is due to the tight spiral packing of the buds (Fig. 1A). This apparent asymmetry is lost at anthesis as the tepals spread. The tepals in *X. tenax* are cut off more directly than in *X. asphodeloides*. The inner and outer tepals of *X. tenax* are equal, whereas in *X. asphodeloides* the inner tepal are slightly narrower and longer than the outer tepals (subequal). Also in the latter, there is a shallow floral tube that is formed by the cohesion of the tepal margins and the adnation of the six stamens (epitepaly) (Fig. 8C). The pedicels are directed outwards during anthesis, whereas in fruit, the pedicels tend to be erect in both species (Fig. 1).

The vascularization of the two tepal whorls is remarkably similar in both species. The outer tepal supply can be traced to the lowest levels of the pedicel where three fusion bundles were formed. Likewise, the inner tepal supply has its origin in the midpedicel zone, again in the formation of three different fusion bundles. An outer tepal supplying bundle is 60° from an inner tepal supplying bundle. The transition from pedicel to receptacle is noted by a sudden increase in cross-sectional area (Figs. 3D–F, 4D–F). As this area increases, three of the smaller outer bundles, which are 120° apart depart outwardly radially. As these three bundles approach the periphery of the receptacle, each undergoes a double radial division. This division results in an outer tepal median (OTM) and two outer tepal laterals (TL) (Figs. 3D–E, 4D–E, 9). The OTM shares the same radius as its parental tepal supplying bundle.

As the three outer tepal supplying bundles divide, the remaining

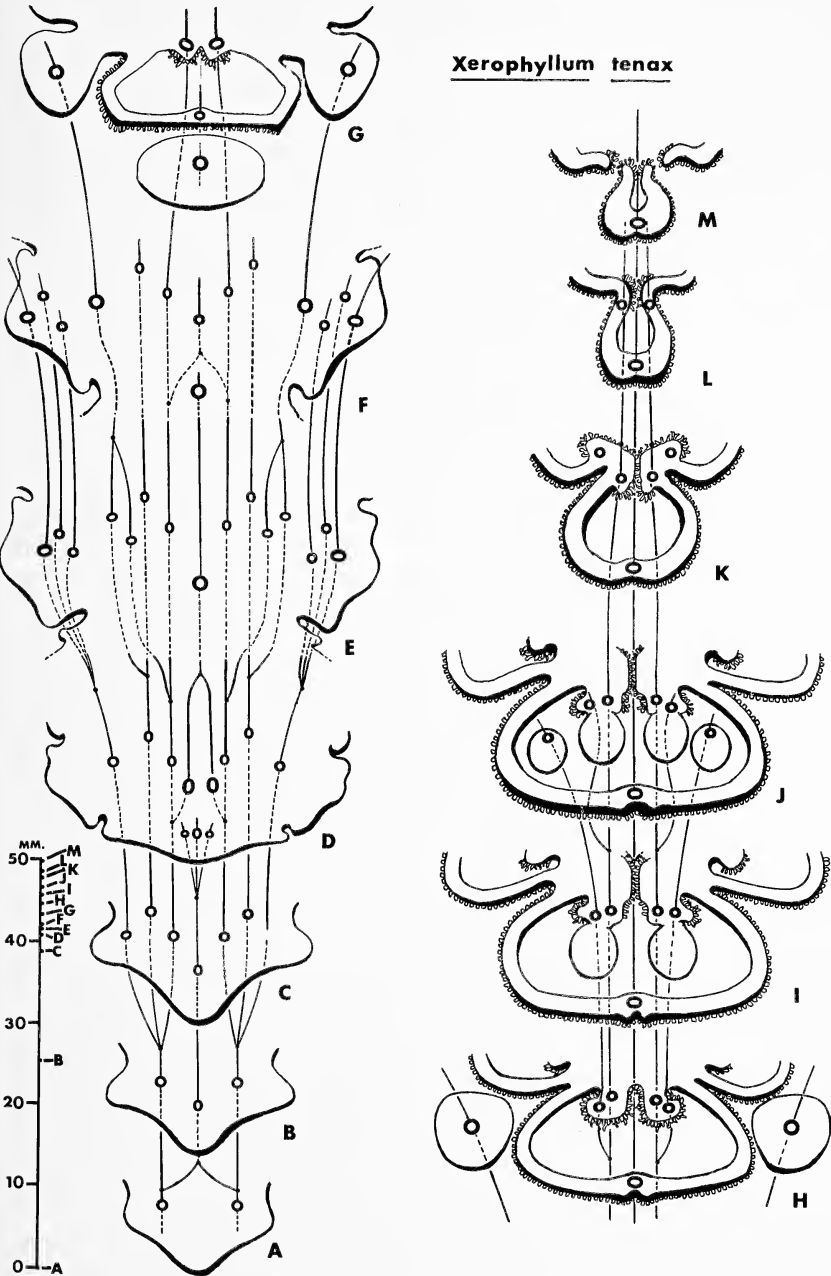


Fig. 4.—*X. tenax*, cross-sections of Fig. 3 after transformational projections with selected vascular bundles connected, lettered cross-sections correspond to those in Fig. 3 and to their relative position on the sectioning scale.

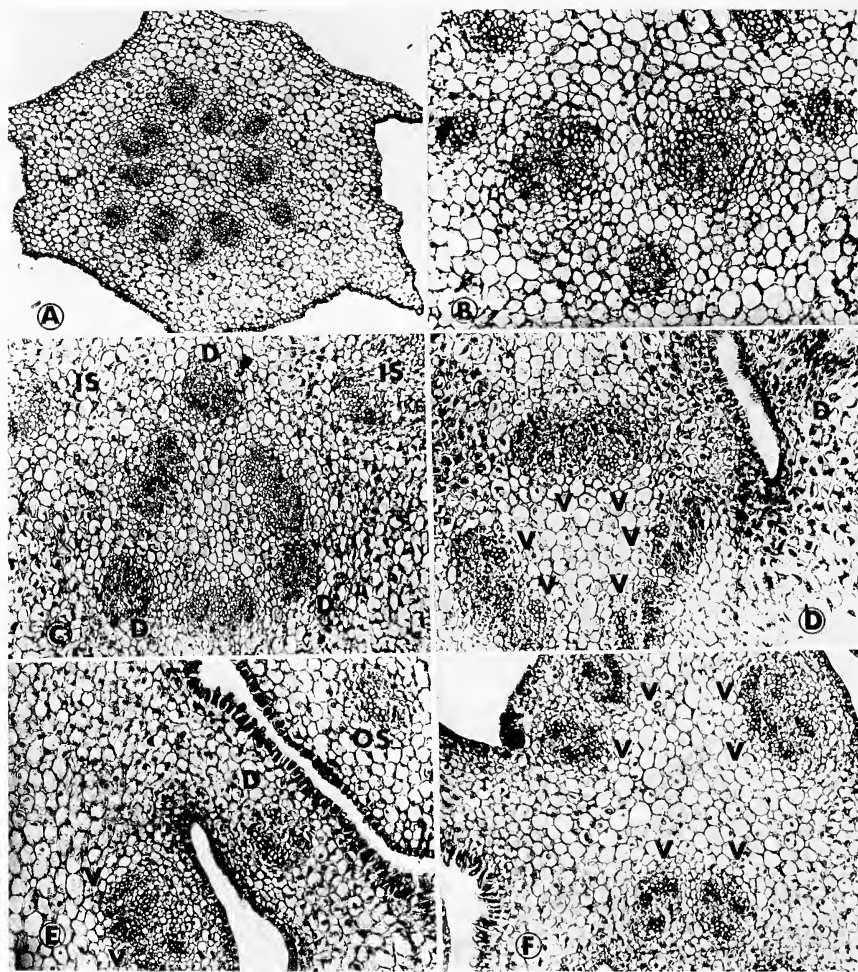


Fig. 5.—Cross-sections of the pedicel, receptacle, and gynoecium base of *X. tenax*. A) Upper pedicel showing the six outer (smaller) and six inner (larger) bundle configurations. Flowering pedicel lacks sclerenchymatous sheath (25 \times). B) Enlargement of A, three smaller and two larger (compound) bundles are indicated, smaller bundles establish the tepal supplies directly (50 \times). C) Receptacle-gynoecium base showing the departure of three dorsals (D) and two inner stamen traces (IS), there is a paired set of bundles remaining between each dorsal (40 \times). D) Section above C, the three paired bundle sets as the ventrals (V) with normally arranged xylem and phloem, locules opening (50 \times). E) Section above D, ventral (V) conducting elements reversed, outer stamen (OS) trace along the same radii as dorsal (D), filament base cut off from the papillae-covered outer carpillary wall (50 \times). F) Solid central gynoecial base showing the six positioned ventrals (V) (50 \times).

three smaller outer bundles also move outward. These three tepal supplying bundles are also compound fusion products and share a common level of pedicel origin. As these three bundles approach the receptacle periphery, they also undergo a similar double radial division, which results in an inner tepal median (ITM) and two inner tepal laterals (TL) (Figs. 3D-E, 4D-E, 9).

Both the outer and inner tepals in *X. tenax* and *X. asphodeloides* are supplied by a three-bundled (trace) pattern of vascularization. Additional radial divisions occur within the laminal surface of the tepals, but these divisions only involve further subdivision of the laterals and not the medians. Once a lateral or its branch is established, there is no terminal cross-innervation of tepal traces.

A differential in the number of lateral divisions exists between the outer and inner whorls. The number of divisions determines the number of veins or traces within a given tepal. In *X. tenax*, the outer tepals usually have five veins, for example, two laterals plus median plus two laterals, due to two radial divisions among the laterals, whereas the inner tepals of this species usually have seven veins, for example, three laterals plus median plus three laterals, due to four radial divisions among the laterals. In *X. asphodeloides* a similar pattern of five veins per outer tepal and seven veins per inner tepal is also observed, but occasionally a five- or six-veined inner tepal is seen. This reduced tepal vein number is directly due to the lack of sequential radial division in a somewhat smaller tepal. The tepal shapes of the two species are similar, only their sizes differ.

Stamens and Their Vascularization

Both species of *Xerophyllum* have similar patterns of stamen vascularization. At the level of stamen trace formation in the receptacle, there are six large inner bundles, which are continuous along their same axes into the pedicel, and six alternating outer bundles, which departed as the tepal supply (Fig. 9). Gaps are left among the radii of the departing tepal supply bundles (Figs. 3D-F, 4D-F, 9), and it is along these gap-radii that the stamen traces are formed.

The three outer stamen traces (OS) are formed first. Each is formed vis fusion of two lateral branches from two different larger inner bundles (Figs. 3D-E, 4D-E, 9). This fusion occurs along the outer tepal radii and closes the three gaps left by the departing outer tepal supply. The three inner stamen traces (IS) have a similar origin as the outer stamens (OS), that is, lateral branches and fusion (Figs. 3E-F, 4E-F, 9). Their fusion is, however, along the radii of the departing inner tepal supply. The two stamen whorls are separated vertically in their level of origin. The three stamens in both cycles are fusion products, and frequently in filament cross-section, their bifid condition can be seen.

The six remaining inner bundles which branched to form the stamen supply continue upward along the same axes, and subsequently establish the total gynoeceal supply (Fig. 9).

In both species, the stamens equal or exceed their respective perianths. The filaments of *X. tenax* are longer (7.5–9.5 mm) than those in *X. asphodeloides* (4.5–6.5 mm). The filaments of both are also hypogynous and freed directly. There is a limited amount of epithecal in *X. asphodeloides* (Fig. 8C). The freeing of the three inner stamens from the receptacle-gynoeceal wall opens three triangular wedges in the gynoeceal outline (Figs. 3G–I, 4G–I). These spaces become the regions of the unfused septal indentations (Figs. 7C, 8D). At this level, the locules have already opened and the dorsal bundles are positioned.

The anthers are attached at their mid-length point and are not basifixed as is often reported (Fig. 7C–F). There is no confluence of thecae terminally. The connective tissue begins in the mid-length region and is continuous to the anther's tip. The stamen traces (OS and IS) are continuous through the connectives. Dehiscence is via lateral slits (extrorse). Rotation of the anthers is possible due to the mid-level attachment of the filiform filaments. The endothecium cells of the anthers sacs have banded thickenings. The filaments diverge, ca. 30–45°, from the vertical gynoeceal axis, and thus create a wide, outer pollen dispersal zone.

Gynoeceum and Carpel Vascularization

Both *Xerophyllum tenax* and *X. asphodeloides* have an ovate, tri-carpellate gynoeceum with deep septal indentations, dorsal grooves and three free, recurved styles. Raphides are present in the outer carpellary walls (pericarps) of both species. Raphide distribution increases with maturity. In both species, the carpellary epidermis, which includes the outer surface of the septal indentations, has a dense covering of papilloid cells. This epidermal modification is more pronounced in *X. tenax* than in *X. asphodeloides* (Figs. 6C–E, 8D–E).

The septal indentations are formed near the receptacle-gynoeceum base, as the inner stamens are cut off (Figs. 3G–H, 4G–H). The three indentations extend to the three free styles which are freed along the septal radii. The two carpellary margins, which subtend a given indentation are fused only at their innermost tips. This is the only anatomical evidence for carpellary fusion within the gynoeceum.

A dorsal groove (notch in cross-section) runs the length of the three carpels (Figs. 3, 4). The dorsals are broadly crescent-shaped (bifid) throughout their gynoeceal course (Figs. 6F, 8D–E). There is no branching of the dorsals (Fig. 9). The fruit is a loculicidal capsule, because the locules are opened along the dorsal grooves. The dorsal

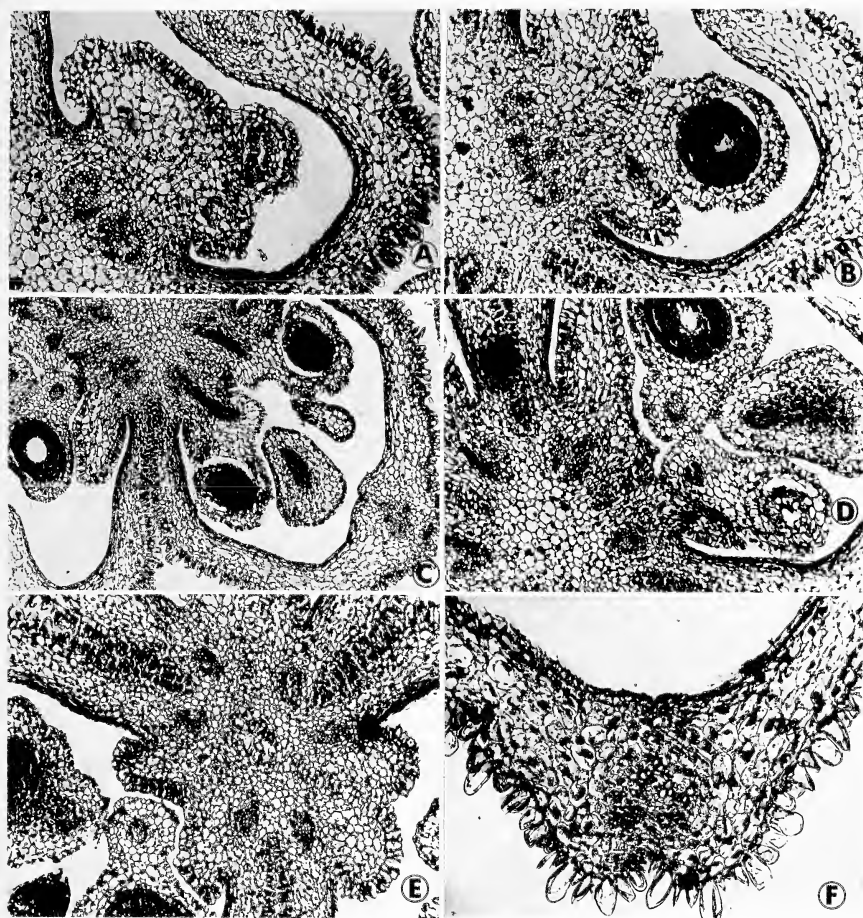


Fig. 6.—Gynoecium cross-section in *X. tenax*. A) Fused septal wing tips protruding into locules, papillose cells on surface of the wing tips, which differ from those lining the locule and the carpellary epidermis, both ventrals reversed (50 \times). B) Each ventral divides with one half continuing upwards and the other half supplying the ovules of the lower tier, septal wing tip margins modified into obturators (50 \times). C) Second tier ovule supply, funicular traces departing to supply colateral ovules, deep septal indentation evident (37.5 \times). D) Second subdivision of ventrals, one division product supplies the second ovule tier (lacking in *X. asphodeloides*), whereas the other continues upwards into the stylar area (50 \times). E) Six ventrals (V) continuing upwards after second tier ovule supply, obturators still present and the inner central area subdivided along the septal radii creating the unilocular gynoecium (50 \times). F) Enlargement of dorsal notch over the dorsal bundle, also showing the outer epidermal papillae and the small, thin-walled cells lining the locule (60 \times).

bundles are physically divided during the mechanical opening of the locules.

A central ring of six bundles remains in the gynoecium base following the formation of the inner stamen traces. At this level, all of the stamen traces have departed along the radii between these remaining six bundles. One final planar division that involves all six bundles occurs. This division is radial. There are 12 resulting branch bundles with six of the 12 branches fusing in pairs along the OTM-OS radii. The three resulting fusion products are the dorsals (D) (Figs. 3F, 4F, 5C). The dorsals (D) depart directly and horizontally along the OTM-OS radii under the yet unopened locules. Soon after the dorsals reach the carpellary margins, the outer stamens are cut off. The three dorsals do not branch in their vertical ascent to the three free styles (Fig. 9).

Six bundles remain in the central gynoecial area after the formation of the dorsals (D) (Figs. 3G, 5C-F). These bundles are the remaining half-strands of the last planar division (Fig. 9). These six bundles directly establish the ventral supply by moving inward radially along the three septa in three paired sets. There is no fusion within each paired set. (Were they to fuse, it would be analogous to the formation of the dorsals.) At this level, the ventrals have normally arranged xylem and phloem, like the dorsals. The two ventrals, which supply the ovules of a given carpel, are continuous at a lower level with the bundles that branched to form the dorsal of that same carpel (Fig. 9). Neither septal axials nor ventral plexuses are involved in the ventral vascularization.

The two paired ventrals (V) along each septal axis disassociate and move apart laterally. With this movement, there is a reversal of the xylem and phloem of all the ventrals (Fig. 5C-E, 6A).

Following this reorientation, there are two ventrals with reversed bundles opposite the locules and dorsals. Concurrent with this ventral reversal, there is an inturning of the septal wing tips to the locules. The inturned margins, for example, obturators, are covered by papiloid cells and are part of the stigmatoid tissue system. The cells, which line the locules, on the other hand, are small, thin-walled, and closely packed (Figs. 3G-J, 4G-J, 6A-F, 8D-E).

The major difference in gynoecial vascularization between *X. tenax* and *X. asphodeloides* is in the number of ovules and how they are supplied. In *X. tenax*, there are consistently four ovules in each carpel (Figs. 3, 4, 6C-D, 9), whereas *X. asphodeloides* consistently has two ovules per carpel (Fig. 8D). Consequently, *X. tenax* has a significant sexual reproductive advantage over *X. asphodeloides*. There are twice as many flowers per raceme and twice as many ovules (seeds) per carpel in *X. tenax* than in *X. asphodeloides*.

The funicular traces (F) in both species are collateral. The seeds of *X. asphodeloides* (two per carpel) are erect and basally attached (Fig.

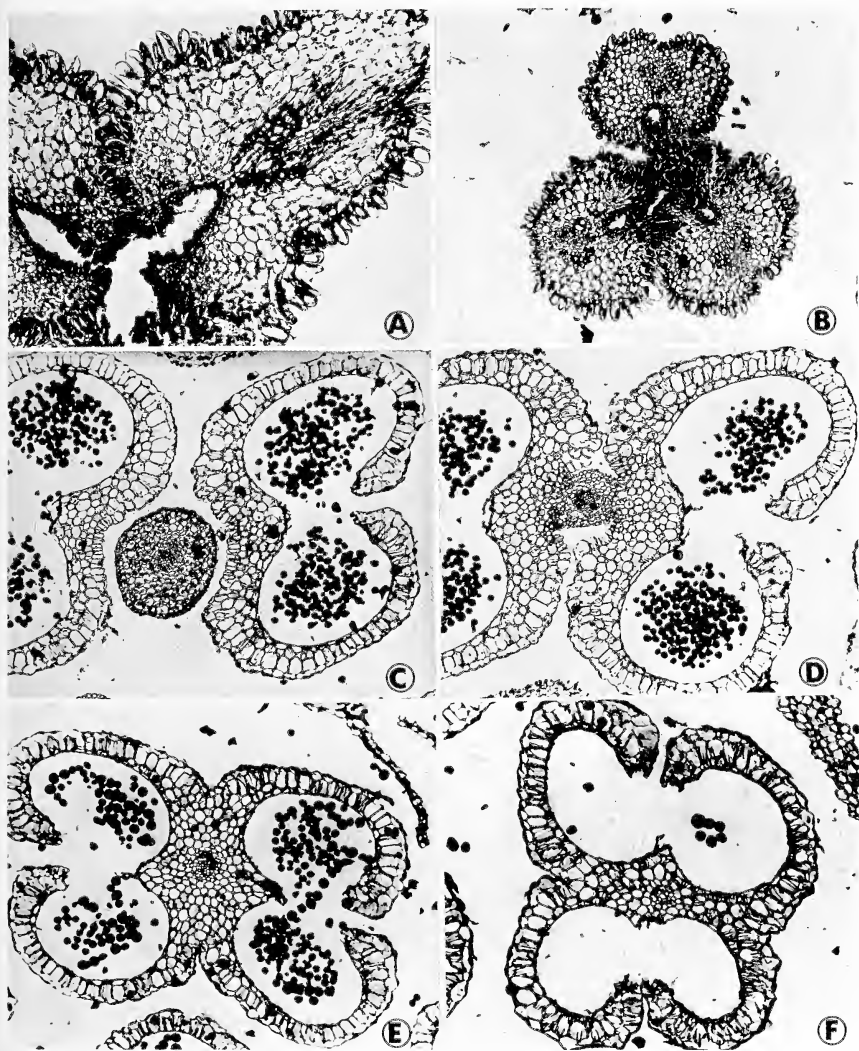


Fig. 7.—Stigma and anther cross-sections in *X. tenax*. A) Upper gynoecium showing common stylar canal, dorsal, and ventrals present (50 \times). B) Three styles freed along the septal radii, outer wall papillae similar and continuous with that of the carpels, septal wing tip papillae different (40 \times). C) Lower anther cross-section showing the free filament surrounded laterally by the two anther sacs, each sac has two chambers and dehiscence via a lateral slit, the outer anthers are similar to the inner anthers (20 \times). D) Section above C, filament attached to the two anther sacs at the midanther length (20 \times). E) Section above D, stamen trace centered in connective, lateral slits still in same position (20 \times). F) Section above E, connective and stamen trace still present, no terminal confluence of chambers (20 \times).

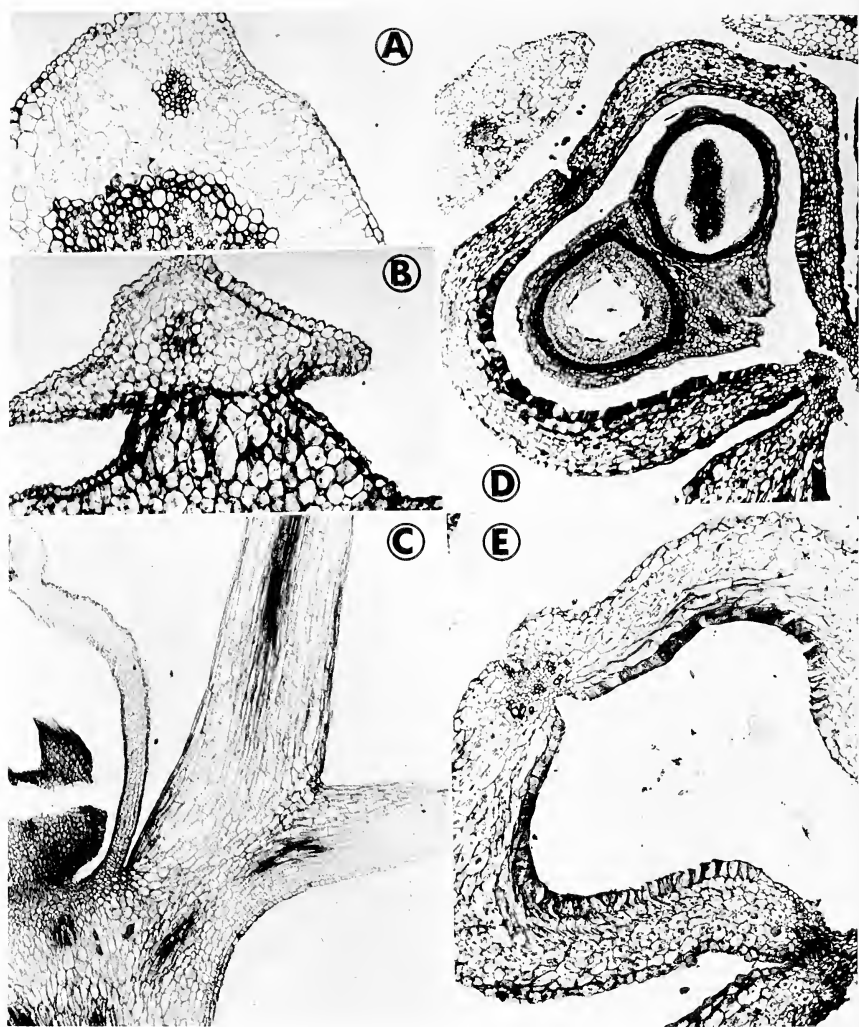


Fig. 8.—Selected floral sections of *X. asphodeloides*. A) Partial pedicel cross-section showing an adnate bract with a single vein, pedicel from the upper portion of the raceme (15 \times). B) Section above A showing the freeing of the bract at midpedicel length (15 \times). C) Longitudinal section showing the degree of epitepaly between an outer stamen and tepal, no similar degree of epitepaly occurs in *X. tenax* (30 \times). D) Mid-gynoecium cross-section showing the two collateral ovules within a locule; a dorsal notch, septal indentation and a central interocular connection are evident (20 \times). E) Upper gynoecium cross-section showing a bifid dorsal, the dorsal notch and non-papilloid epidermis of the carpellary outer wall; the locule lining cells are similar to those in *X. tenax* (35 \times).

2D), whereas the seeds of the second tier in *X. tenax* (two additional per carpel) are variable in their packing. The seeds of both species are similar in size and shape. They are three-angled and lack terminal wing tips and appendages.

The division of the central gynoecial base continues between the inturned obturators of each locule. This division lags behind the opening of the three locules, but definitely interconnects the three locules along the dorsal radii (Figs. 6E–F, 8D–E). The tricarpellate gynoecium in *Xerophyllum* is, therefore, potentially unilocular (Figs. 3–4). The septal wing margins, however, remain fused along the septal radii, and are anchor shaped in cross-section along the vertical floral axis. The axial faces of the appressed, inner septal margins are covered by interdigitating papillae. These papillae, as those on the obturators, extend from this basal area, past the level of ovule supply, to the inner surface of the three free stylar branches. These papilloid cells stain differently from the papilloid cells of the carpellary epidermis. The inner papillae form a continuous, internal stigmatoid support system for the canalized growth of the pollen tubes.

In bud the three free linear styles of both species are initially erect, but at anthesis they are recurved outwards along the dorsal radii. The stylar arms are narrow and flexible. The inner exposed bases of these styles are lined with papillae. An opening between the styles is continuous with the upper unilocular cavity of the gynoecium (Fig. 7A–B). The style lengths in *X. tenax* are between 4.5 to 6.0 mm, whereas those in *X. asphodeloides* are not too dissimilar, 4.0 to 5.5 mm. The pollination system in both species is relatively open to both out- and inbreeding, because the versatile stamens are arranged in a circle around and above the divergent and recurved stylar arms.

SUMMARY AND CONCLUDING REMARKS

The floral vascularization of both species of *Xerophyllum* is remarkably similar from the pedicel up through the tepals, stamens, and gynoecia. A species specific difference occurs in the gynoecia, however. *Xerophyllum asphodeloides* consistently has two ovules (seeds) per locule, whereas *X. tenax* has four ovules (seeds) per locule. The vascular difference associated with ovule number is merely an additional radial division of the ventral strands in *X. tenax*. The overall flower and fruit size of *X. tenax* is proportionately larger than in *X. asphodeloides*. The floral vascularization of *X. asphodeloides* represents a reduced and simplified version of that in *X. tenax*. Because of a greater ovule and seed number in *X. tenax*, it consequently has a greater sexual reproductive advantage.

The tepal supplying bundles are established in the lower halves of the pedicels. The outer tepal supplying bundles are established via

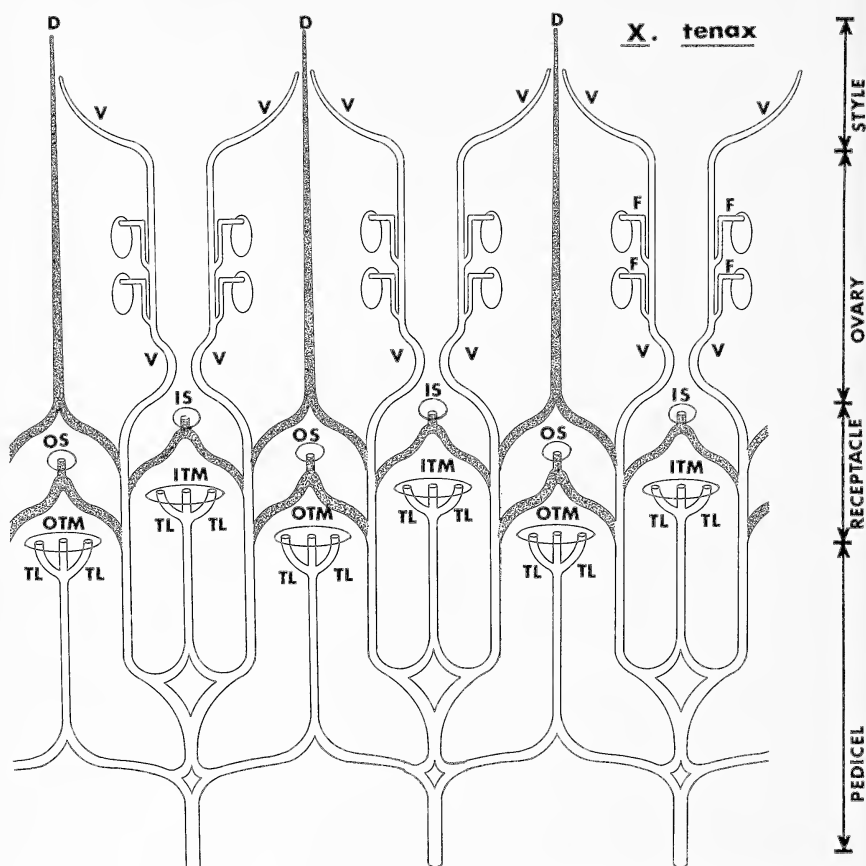


Fig. 9.—Roll-out longitudinal summary diagram for the floral vascular anatomy of *Xerophyllum tenax* [*Xerophyllum asphodeloides* differs in having a single funicular trace (F) from each ventral (V), not two.] The various bundles are labeled with text introduced letter codes: OTM = outer tepal median, ITM = inner tepal median, TL = tepal lateral, OS = outer stamen, IS = inner stamen, D = dorsal, V = ventral, and F = funicular.

fusion near the pedicel attachment to the raceme axis. The inner tepal supplying bundles are established via fusion, but in the midpedicel region. The receptacle base has a double ring of 12 bundles, that is, six outer ring bundles (the tepal supply formed in the pedicel), and six inner core bundles. The bundles of the two rings are on alternate radii.

Each tepal of both whorls receives a similar compound bundle. Each compound bundle divides to form a median and two associated laterals before its tepal is cut off. The pattern of vascularization is the same for both the outer and inner tepals. In mature flowers of both species,

there is a difference in the number of laterals in the outer and inner tepals. This is due to a differential in the number of radial divisions amongst the outermost laterals. *Xerophyllum tenax* has five veins, that is, two laterals plus median plus two laterals in its outer tepals; and seven veins, that is, three laterals plus median plus three laterals in its inner tepals. A similar pattern with a greater vein number in the inner tepals than in the outer tepals also occurs in *X. asphodeloides*.

The stamen traces of both the outer and inner whorls are fusion products. They arrive via radial branches from the inner ring bundles which fuse. The filaments are freed directly from the receptacle; there is a limited amount of epitepaly in *X. asphodeloides*. The filaments within each species are equal in length, dilated basally and filiform terminally. The anthers are versatile, attached at midlength, laterally dehiscent and not confluent terminally.

The basal gynoecium supply in both species of *Xerophyllum* is relatively simple. The gynoecial base has six bundles. The three dorsals are formed as fusion products via side branches from these six bundles. After the establishment and localization of the three dorsals, the six continuing parental bundles associate in three pairs, as ventrals, along the septal radii. The ventrals are characterized by a reversed arrangement of their conducting tissue. The six ventrals directly supply the ovules of the three carpels.

The placentation in *Xerophyllum* has usually been described as axillary and associated with a trilocular gynoecium, but the placentation is actually parietal due to both a pulling apart of the septa along their axial faces and to an inward unrolling of the inner septal (placental) margins as far down as the base of the ovary. The tricarpellate gynoecium is therefore unilocular.

The fruit in *Xerophyllum* is a loculicidal capsule. The flowering gynoecium has dorsal grooves along which the locules are subsequently opened. Septal indentations are also present, but there is no indication of septicidal splitting. The three carpels are fused only along the inner septal margins and the basal wing tips. Rhaphides occur in both species, especially in their gynoecia. In *X. tenax*, the outer carpellary wall has a papilloid epidermis, this is lacking in *X. asphodeloides*. A stigmatoid tissue system composed of a second papilloid cell type was described. These cells are continuous from the three free stylar tips down the common style and into the unilocular ovary along the axial, appressed faces of the inner septal margins.

Anderson (1940) who followed the Englerian system summarized the vascular condition in *Xerophyllum asphodeloides* as follows: "The origin of (all) the traces is most like that of *Veratrum*, and the carpels are as free as in that genus; but there is no perigyny and the receptacle is rather elongated; there are but two ovules. All in all this is the most

primitive member of the group (Melanthioideae), anatomically; and except for the reduction in ovule number there are no advanced characters present." Furthermore, the reduced ovule number in *X. asphodeloides* is part of an evolutionary reductional series from the four ovules per locule condition in *X. tenax*.

Proper and critical assessment of the tribal position of *Xerophyllum* in both the Englerian (Engler, 1888; Krause, 1930) and Hutchinsonian (Hutchinson, 1934) systems must await further anatomical work among the other primitive members of the Melanthioideae. Such work is in progress.

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The author would like to thank the M. Graham Netting Research Fund of the Carnegie Museum of Natural History for supporting this research through a grant. Special thanks are also due Mr. Robert A. Osterman, Ms. Julia Siy-Hian and Ms. Linda E. Plowman for their technical assistance in the preparation of the slide material, and to Ms. Pamela J. Leopold and Ms. Nancy J. Perkins for their artistic effort in the figure production.

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VASCULAR FLORAL ANATOMY OF *HELONIAS BULLATA* (LILIACEAE-HELONIEAE), WITH A COMPARISON TO THE ASIAN *HELONIOPSIS ORIENTALIS*

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ABSTRACT

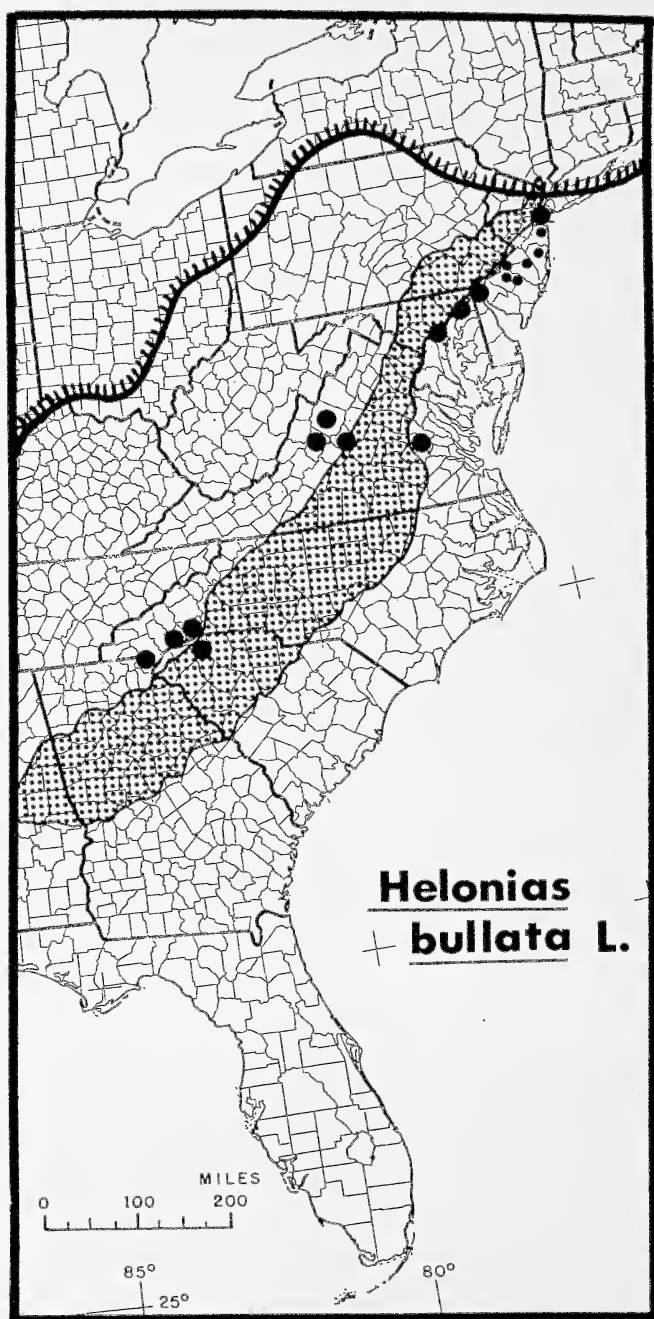
The vascular floral anatomy and carpel morphology of the monotypic, American *Helonias bullata* are presented and discussed in relation to the vasculature and morphology of the Asian *Heloniopsis orientalis*. *Helonias* is the type genus of the liliaceous tribe Helonieae. The vasculature of *Helonias* represents a peculiar type found among the primitive Liliaceae. The pedicel has six free axial bundles. Three of these pedicel bundles independently establish via radial divisions the outer tepal, the outer stamen, and dorsal vasculatures. The three remaining and alternating bundles establish the vasculature for the inner tepals, the inner stamens, and the ventral network. There is no fusion involved in the formation of the various tepal and stamen whorls. The dorsals have a looped path over the extended locule lobes and into the sunken styles, but there is no branching or cross-fusion among the dorsals. The ventral supply has two vertical placentals and a pair of fusion septal axials in each septum. Compound funicular traces arise from each placental in two-ranked rows. The fruit is a loculicidal capsule. The difference in floral vasculature between *Helonias* and *Heloniopsis* is insignificant when it is analyzed from an overall reproductive (sexual) point of view. Additional comparison between the two species strongly supports the position that both species should be maintained in the same tribe.

INTRODUCTION

Helonias bullata L. ("swamp pink") is a rare, monotypic genus of eastern North America with a highly local and dissected range (Fig. 1; Fernald, 1950; Johnson, 1969; Radford et al., 1964). The total known range is below the Pleistocene glacial maxima. This species occurs in acid soils on the older, southern uplands of the Blue Ridge Province in Georgia, North Carolina, and Virginia, and in the newer, northern

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coastal plains of New Jersey (pine barrens), Delaware, Maryland, and Virginia. Locations are significantly scarce in the intervening Piedmont Plateau Province. A single chromosome count of $2n = 34$ (Miller, 1930) has been reported.

Linnaeus' (1753:342) circumscription of *Helonias* included a single species, that is, *H. bullata*. Since Linnaeus, numerous species have been added and later removed from *Helonias*. Today, these species are found in the following genera: *Chamaelirium*, *Veratrum*, *Melanthium*, and *Xerophyllum*. *Helonias* has been consistently treated as a monotypic genus during this century with little taxonomic disagreement on the primitive status of *Helonias* within the primitive subfamily Melanthioideae tribe Helonieae.

The cited Linnaean type locality (1753:342) for *Helonias bullata*—*habitat in Pennsylvaniae paludosis*—probably does not mean a Pennsylvania site, but some low, swampy area, which was frequented by the early botanists out of the port city of Philadelphia. Asa Gray (1859) noted Pennsylvania within the range of *Helonias*, but probably was only indirectly citing Linnaeus (1753). There are no Pennsylvanian collections for this species at the Gray Herbarium (GH), New York Botanical Garden (NY), Philadelphia Academy (PH), Carnegie Museum (CM), Missouri Botanical Garden (MO), University of Wisconsin-Madison (WIS), and University of Michigan (MICH). Johnson (1969), who surveyed an additional 36 herbaria from eastern North America, does not indicate a Pennsylvanian location on his *Helonias* map. Britton and Brown (1913) noted that this species was "not definitely known to grow wild in Pennsylvania." Extinction in the 18th and 19th centuries from a Pennsylvanian type locality is however a distinct possibility. It appears most likely, however, that the type locality was near Philadelphia. A probable area would be across the Delaware River from Philadelphia in the pine barrens of New Jersey (Fig. 1). Numerous endemics are known from this area (Harshberger, 1916). There are too many ephadic and biotic differences between eastern Pennsylvania, that is, the area surrounding Philadelphia, and the New Jersey pine barrens (Harshberger, 1916; Stone, 1912; Taylor, 1912; Buell and Cantlon, 1950) to support an ecological argument for a Pennsylvanian type site.

This paper will present the vascular floral anatomy of *Helonias bullata* as part of a continuing series of investigations on the vasculature

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Fig. 1.—Distribution of *Helonias bullata* based in part on Johnson (1969) and Radford et al. (1968). New Jersey locations (small dots) based on specimens at Carnegie Museum (CM). Wisconsin glacial maxima (bridged line) indicated, as well as the Piedmont Plateau Province (dotted screen). There are no known specimens from Pennsylvania.

Table 1.—*Character Comparison between Helonias bullata L. and Heloniopsis orientalis (Utech and Kawano, 1978; in part).*

Character	<i>Helonias bullata</i>	<i>Heloniopsis orientalis</i>
Root system	Stout rootstock with numerous fibrous rhizomes	Stout rootstock with numerous fibrous rhizomes
	Offset plants easily produced via rhizomes	Offset plants easily produced via rhizomes
Basal leaves	Evergreen, dark green, thin, finely parallel nerved; in basal rosette	Evergreen, dark green, thin, finely parallel nerved; in basal rosette
	Oblong-spatulate to oblanceolate; base attenuate; tip acute	Oblong-spatulate to oblanceolate; base attenuate; tip acute
	Large leaves: (9.0)–12–25–(35) cm by (1.5)–2.0–4.0–(5.0) cm	Larger leaves: (7.0)–9–25–(35) cm by (1.5)–2.0–4.0–(5.0) cm
Inflorescence	Dense terminal spike-like raceme with 40 to 60 flowers	Terminal raceme with 4 to 8 flowers; umbelloid in bud
	Average flower number: mean = 51.3 flowers/raceme	Average flower number: mean = 4.7 flowers/raceme
	Scape below flowers with short bract-like leaves; persistent	Scape below flowers with short bract-like leaves; persistent
	Scape hollow in cross-section at anthesis	Scape hollow in cross-section at anthesis
	Flowering raceme ovoid to cylindrical; post-anthesis internodal elongation	Flowering raceme spherical to ovoid; postanthesis internodal elongation
Pedicel	Pedicels ebracteate	Pedicels bracteate, but soon deciduous
	Pedicels glabrous, fluted (six-lobed in cross-section)	Pedicels glabrous, fluted (six-lobed in cross-section)
	Pedicel length: at anthesis less than perianth length, elongating in fruit Anthesis: 4.0–6.0 mm; mean = 5.2 mm Fruit: 6.5–8.5 mm; mean = 7.2 mm	Pedicel length: at anthesis less than perianth length, elongating in fruit Anthesis: 17.0–27.0 mm; mean = 22.5 mm Fruit: 20.0–33.5 mm; mean = 28.0 mm

Table 1.—(Continued)

Character	<i>Helonias bullata</i>	<i>Heloniopsis orientalis</i>
Perianth (OT = outer tepal; IT = inner tepal)	Light lilac-purple to pink at anthesis	Light lilac-purple to pink at anthesis
	Persistent; greenish yellow to brown at maturity	Persistent; greenish yellow to brown at maturity
	Six-parted, divergent, non- ciliated; spatulate to oblong; equal; free	Six-parted, divergent, non- ciliated; spatulate to oblanceolate; equal; free
	Tepal length: 5.5–8.5 mm; mean = 6.7 mm	Tepal length: 14.0–14.5 mm; mean = 14.3 mm
	Tepal width: 1.8–2.2 mm; mean = 2.0 mm	Tepal width: 3.0–3.5 mm; mean = 3.25
	Tepal L/W ratio: 3.35	Tepal L/W ratio: 4.09
	Glandless, no basal tepal nectaries	Basal succate nectaries at OT and IT bases
Stamens (OS = outer stamen; IS = inner stamen)	OT: three-nerved (rarely 5) IT: three-nerved (rarely 5)	OT: five-nerved IT: five-nerved
	OT and IT vasculature have single bundle origin; no fusion, only radial division	OT and IT vasculature have single bundle origin; no fusion, only radial division
	Six; filaments filiform, persistent exceeding perianth	Six; filaments filiform, persistent, exceeding perianth
	Inner filaments adnate to ovary wall; outer freed directly and basally	All 6 filaments freed directly at ovary base
	OS length: (filament) 7.0–9.5 mm; mean = 8.5 mm	OS length: (filament) 13.1–13.6 mm; mean = 13.3 mm
	IS length: (filament) 6.6–8.7 mm; mean = 8.0 mm	IS length: (filament) 13.0–13.7 mm; mean = 13.2 mm
	OS and IS bundle simple, direct and no fusion	OS and IS bundle simple, direct and no fusion
	Anthers bluish black (dried); purplish blue (fresh)	Anthers purplish black (dried); purple (fresh)
	Anther length: (anthesis) OS: 1.7–2.2 mm; mean = 2.0 mm IS: 1.7–2.2 mm; mean = 2.0 mm	Anther length: (anthesis) OS: 3.0–4.5 mm; mean = 4.1 mm IS: 3.0–4.4 mm; mean = 4.1 mm

Table 1.—(Continued)

Character	<i>Helonias bullata</i>	<i>Heloniopsis orientalis</i>
Gynoecium	Lateral dehiscence; 2 sacs, four-celled, versatile	Lateral dehiscence; 2 sacs, four-celled, versatile
	Filiform filament attachment below midanther point	Filiform filament attachment below midanther point
	Basal anther lobes divergent	Basal anther lobes divergent
	Tricarpellate, massive basal placentae, unilocular terminally; nonstipitate	Tricarpellate, massive basal placentae, unilocular terminally; nonstipitate
	Dorsal grooves; no septal indentations	Dorsal grooves; no septal indentations
	Raphides present in wall	Raphides present in wall
	Depressed upper ovary with sunken styles	Depressed upper ovary with sunken style
	Styles 3, free, separate to the base, stigmatic down inner surface; tips recurved Length: 3.7–4.9 mm; mean = 4.1	Style fused, filiform, hollow, with capitate stigma that is weakly 3 divided, Length: 18.3–19.0 mm; mean = 18.6
	Obcordate, three-lobed loculicidal capsule; walls thin and chartaceous; irregular septal shredding terminally	Obcordate, three-lobed loculicidal capsule; walls thin and chartaceous; irregular septal shredding terminally
	Seed number: ca. 48 per capsule	Seed number: ca. 540 per capsule
Seeds	Dorsal simple and unfused; looped path over carpel; no branching	Dorsal simple and unfused; looped path over carpel; no branching
	Ventral plexus; 2 placental bundles and 1 septal axial per septum; funicular network with 4 ovule rows per septum	Ventral plexus; 4 placental bundles and 2 septal axials per septum; funicular network with 8 ovule rows per septum
	Appendaged at both ends, linear Length: 3.5–4.8 mm; mean = 4.4	Appendaged at both ends, linear Length: 4.1–5.6 mm; mean = 5.1
Chromosome number	$2n = 34$ (Miller, 1934)	$2n = 34$ (see review—Utech and Kawano, 1978)

of the primitive Melanthioideae-Helonieae (Utech and Kawano, 1978; Utech, 1978*b*). This paper will also complete the preliminary and unpublished account on *Helonias* by Anderson (1940:62–65). Because *Helonias* is the type genus for both an Englerian and Hutchinsonian tribe, that is, Helonieae (Engler, 1888; Krause, 1930) and Heloniodeae (emend.) (Hutchinson, 1934, 1959), respectively, a presentation of the vascular floral anatomy of *Helonias* must precede any intergeneric comparison and tribal evaluation. This report, besides presenting the vascular floral anatomy of *Helonias bullata*, will compare it to that of *Heloniopsis orientalis* (Utech and Kawano, 1978).

MATERIALS AND METHODS

Inflorescences with both flowers and fruits were collected from two different populations—New Jersey: Burlington Co., Ons Hat (Utech 76-512 CM), and North Carolina: Henderson Co., between Bat Cave and Henderson (Utech 77-811 CM). The collected materials were fixed in acetic-ethanol (1:3) for 10 h with subsequent storage in 70% ethanol. Standardized paraffin sectioning (14–16 μ) and staining (saffarin-methylene blue) techniques (Johansen, 1940; Sass, 1958) were used on samples from both populations (10 flowers and 10 fruits of varying ages). As an additional check on these serial sections, whole flowers and fruits were also cleared and stained in a NaOH-1% fuchsin mixture (Fuchs, 1963).

Figs. 2–4 are composite photomicrographs which present the vascular floral anatomy of *H. bullata*, whereas Figs. 5–7 are summary diagrams for the species. No teleological implications are intended in the descriptive ascent and departure of the various floral bundles and traces. These bundles and traces are letter-coded for ease in comparison. This coding parallels that used in our previous liliaceous studies (Utech and Kawano, 1975, 1976*a*, 1976*b*, 1978; Utech 1978*a*, 1978*b*). Table 1 and Fig. 8 compare the vascularization of *Helonias bullata* with that of *Heloniopsis orientalis*. Comparative observations on *Heloniopsis orientalis* (Utech and Kawano, 1978) were recently made in Japan.

OBSERVATIONS

Pedicle Vascularization

In early flower, the racemes of *Helonias bullata* are oblong-ovate in shape. In maturity, there is a significant increase in both the interpedicel spacing, as well as pedicel length (Table 1). The resulting raceme is therefore extremely oblong. Persistent, triangular scale-like bracts occur on the scape. These scape bracts were mistakenly omitted in the 1804 Curtis Botanical Magazine illustration (t. 747).

Tepal and Stamen Vascularization

Vascularization of the six tepals (two whorls of three) and the six stamens (two whorls of three) is via repeated radial division of branches from the basic six pedicel bundles. The resulting branches are simple, direct, and involve no lateral fusion. The six branch bundles that are formed first are actually in two whorls and are separated by a short

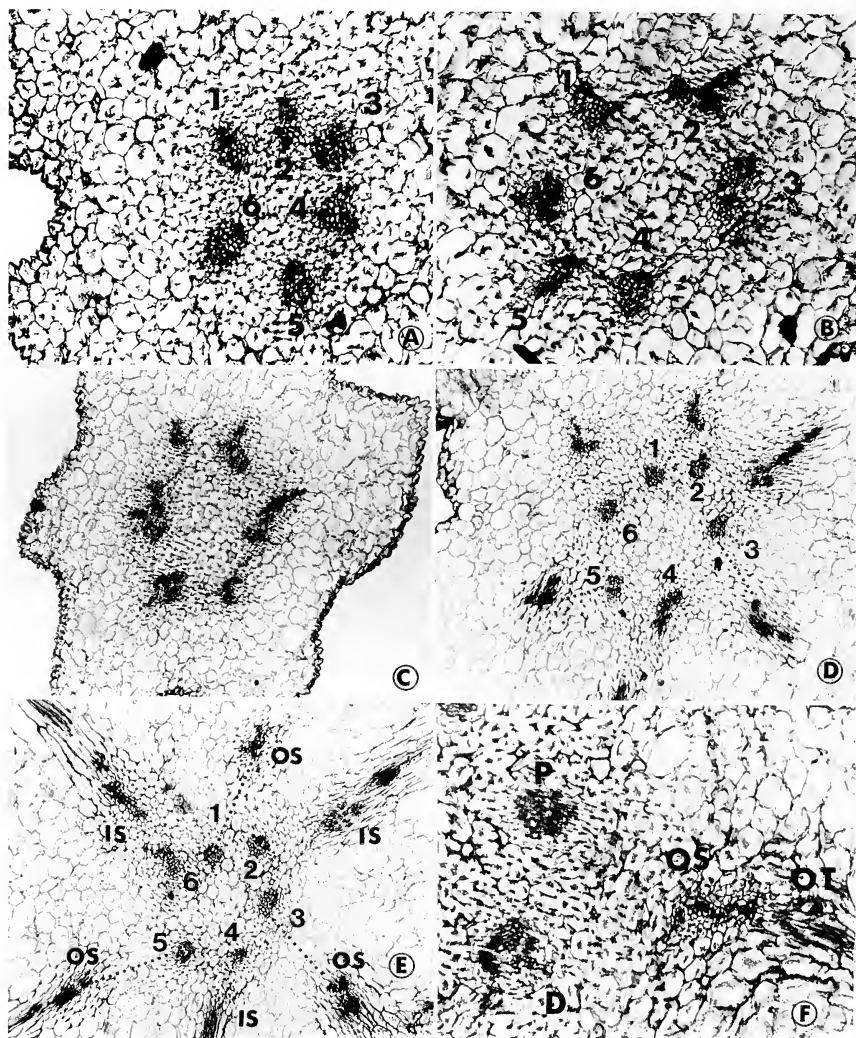


Fig. 2.—Pedicel vascularization in *Helonias bullata*. A) Midpedicel cross-section showing the six bundled vascular configuration and peripheral lobing; bundles numbered (40 \times). B) Cross-section above A showing the partial subdivision of several pedicel bundles; all with normally arranged conducting elements (40 \times). C) Cross-section near level B showing the radial divisions (25 \times). D) Upper pedicel cross-section above C showing the six remaining inner bundles and the six departing branch bundles; bundles numbered (25 \times). E) Upper pedicel-lower receptacle above level D showing the two whorls of common tepal-stamen traces (25 \times). F) Dorsal (D) and common placental (P) established centrally from the inner pedicel bundles and the common tepal-stamen trace subdivided into an outer stamen trace (OS) and an outer common tepal trace (OT) (40 \times).

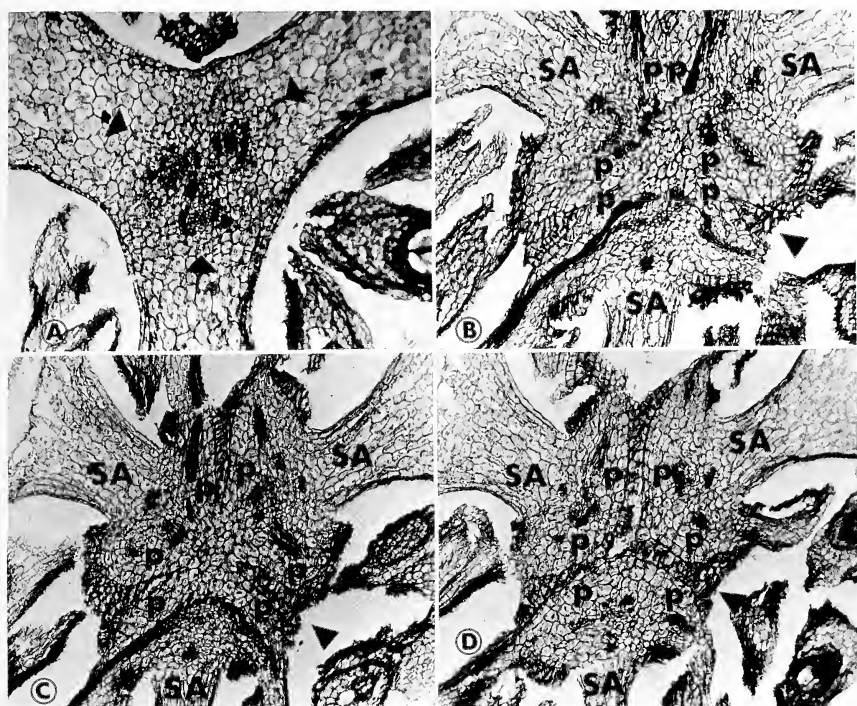


Fig. 3.—Gynoecium base in *Helonias bullata*. A) Septal location of the three basal compound placental bundles; locules open and dorsals positioned (50 \times). B) Cross-section of lower gynoecium central base, which is not divided (triangle); each of the compound bundles of A is divided into a fusion septal axial (SA) and two vertically ascending placentals (40 \times). C) Cross-section above B at mid-gynoecium showing the partial subdivision of the central placentae (triangle); bundles as in B (40 \times). D) Cross-section above C showing the three freed inner septa (triangle) with similar vascularization as B and C (40 \times).

vertical distance. These branch bundles are all formed on the same corresponding side of a given parental (pedicel) bundle (Fig. 2C–D).

A temporary, alternate arrangement occurs in the pedicel among the six larger main bundles, which are along the lobe radii, and the six smaller resulting branches, which are along the sinus radii. This spacing is physically due to the radial division (Figs. 2D–F, 5A–C, 6A–C). However, within a short vertical distance, all the bundles are realigned along the lobe radii (Figs. 2F, 5A–C, 6A–C) with the branch bundles nearest the periphery.

Three of the outer bundles, those formed first and 120° apart along the lobe radii, depart horizontally as the common outer tepal-stamen (OTS) traces. Similarly, the three remaining and alternating outer

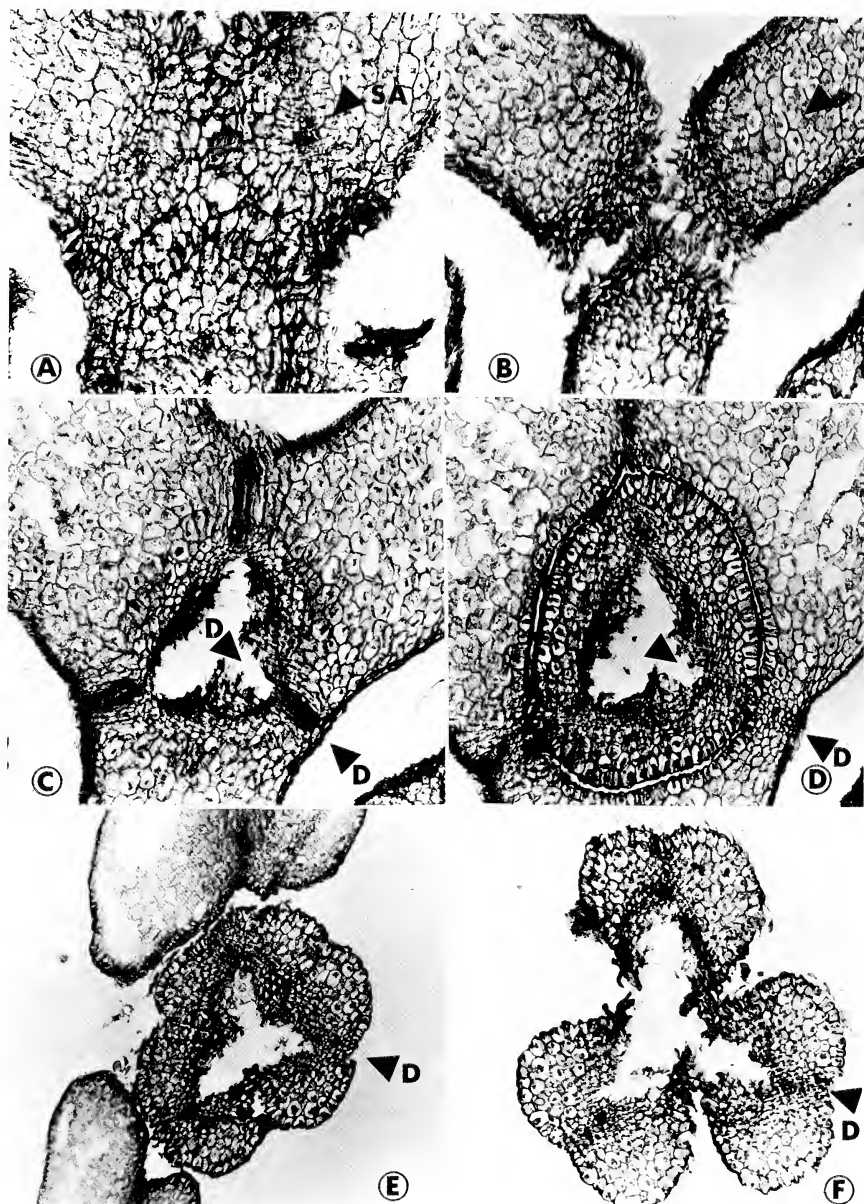


Fig. 4.—Upper gynoecium and styles in *Helonias bullata*. A) Cross-section through upper gynoecium showing the three septal wings with a septal axial (SA; triangle) remaining in each; papillae line the central axis (50 \times). B) Cross section above B showing no septal vasculature (triangle) (50 \times). C) Lateral fusion of the septal wings; bottom of

branch bundles depart horizontally as the common inner tepal-stamen (ITS) traces. As the two whorls of common traces (OTS and ITS) reach the region of tepal attachment, each undergoes a radial division. From this division, each common OTS yields an outer tepal supplying bundle (OT) and an outer stamen trace (OS), and each common ITS yields an inner tepal supply bundle (IT) and an inner stamen trace (IS) (Figs. 5C–G, 6C–G, 7).

Each tepal supplying bundle (OT and IT) broadens prior to a double radial division. This division occurs first among the three OT supplying bundles (Figs. 5D–E, 6D–E), and is followed by a similar type of division among the three IT supplying bundles (Figs. 5E–F, 6E–F). For both whorls, the vascular results are the same—each outer tepal receives a median (OTM) and two laterals (OTL), and each inner tepal receives a median (ITM) and two laterals (ITL) (Fig. 7). Following these divisions, the receptacle base has six bundles which are coaxial with the six pedicle bundles. No fusion is involved in their formation. Significantly, all of the tepal and stamen vasculature can be traced directly to the six free axial pedicel bundles.

Both the inner and outer whorls of flowering tepals are rose-colored and persist into the fruiting stage. In fruit, the color changes to a greenish brown. Tepal length and width of both whorls are essentially the same (Table 1). Basally, all tepals lack sacate nectaries which are characteristic of *Heloniopsis orientalis*. Three is the common vein number for both the outer and inner tepals of *Helonias bullata*. Occasionally, a fourth or fifth vein (bundle) is observed in either of the tepal whorls, but this is merely due to an additional radial division within the laminal surface. *Heloniopsis orientalis* commonly has five veins in its tepal whorls (Table 1). The filament bases are completely free from the tepals, because there is no epitepaly in *Helonias*. The three inner filaments are adnate to the outer, basal gynoecial wall (Figs. 5D–G, 6D–G). The three outer filaments are not.

There is a difference in the filament length between the outer and inner whorls (Table 1). This is due to the adnation of the inner filaments. The overall anther heights are, however, similar. At maturity, the filaments diverge at an angle of 45° relative to the vertical axis of the gynoecium. The anthers are short in *Helonias* (Table 1), but similar in length between the two whorls. The four-lobed anthers are laterally

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sunken style (50×). D) Cross-section above D showing the central style surrounded by the laterally fused septal wings of the upper ovary; a given dorsal (D) observed in two places (triangles) (50×). E) Cross-section above the gynoecium showing the three free styles each with a dorsal (D) and the inner surface lined with stigmatoidal papillae (40×). F) Section above E showing the three styles (40×).

dehiscent and versatile. The filaments are attached slightly below the anther's mid-length point. Below the point of attachment, there is a tendency for spreading of the two lower, separated halves of the anther. Because the anthers are short, but definitely four-lobed, they appear as though they are terminally confluent due to the basal spreading. This they are not. The anthers of *Helonias bullata* differ only in length and color from those of *Heloniopsis orientalis* (Table 1: Utech and Kawano, 1978).

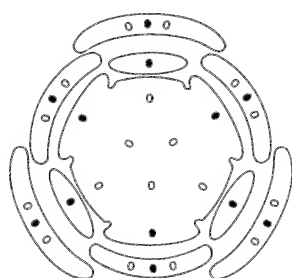
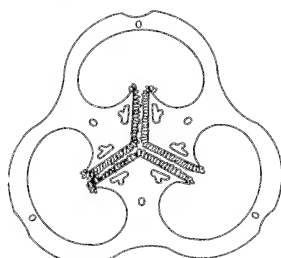
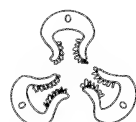
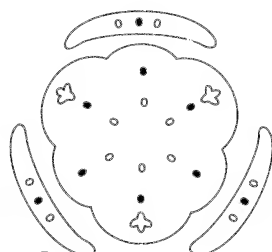
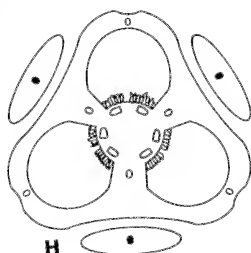
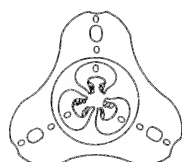
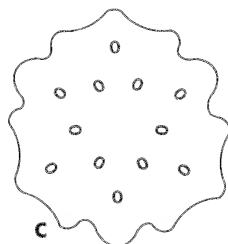
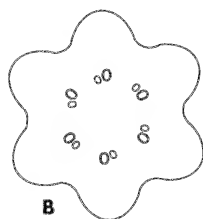
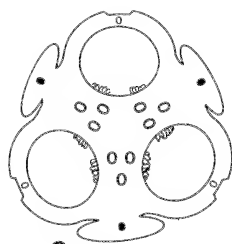
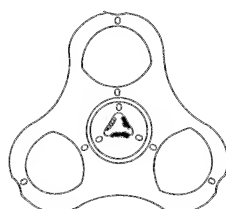
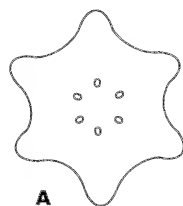
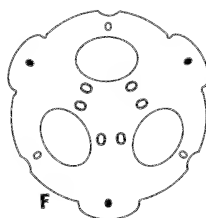
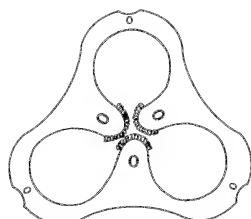
Gynoecial Vascularization and Carpel Morphology

Dorsal and ventral supply.—Following tepal and stamen vascularization, the central gynoecial base contains six simple bundles. These bundles are along the outer tepal median-outer stamen (OTM-OS) and the inner tepal median-inner stamen (ITM-IS) radii. The three bundles along the OTM-OS radii become the three dorsals directly without any fusion. The three remaining and alternating bundles, which are along the ITM-IT radii, determine the ventral vascular system (Fig. 3A). The latter are not formed as directly as the former. At this basal level, the gynoecium is relatively broad and the six bundles are widely spaced and quite distinct with normally disposed xylem and phloem.

As the three dorsals (D) depart peripherally under the three unopened locules, the three remaining bundles move inwards along the septal radii. The dorsals remain unbranched throughout their vertical

→

Fig. 5.—Selected floral cross-sections of *Helonias bullata*. A) Midpedicel cross-section showing the fluted periphery and the six bundled vascular configuration. B) Upper pedicel showing the radial subdivision of the six pedicel bundles. C) Pedicel-receptacle base showing the origin of the tepal and stamen vasculature. D) Receptacle base showing the three outer freed tepals with a median (OTM) and two laterals (OTL). All six stamen traces are formed with six inner bundles remaining. E) Upper receptacle-lower gynoecial base showing the six free tepals each with a median and two laterals; the three outer stamens are freed, whereas the three inner stamens are adnate to the outer carpellary wall; there is no epitepaly; three of the inner six bundles have departed outward along the OS-OTM radii to become the dorsals (D), whereas the remaining three have moved inwards along the septal radii to establish the ventral supply. F) Gynoecial base showing the opening of the three locules; dorsals (D) established; ventral placental pair (P_1 and P_2) established in each septum; three inner stamens adnate to carpellary wall; dorsal grooves evident. G) Lower gynoecial base showing the three fusion septal axials (SA) between the placental (ventral) pairs; inner stamen still adnate. H) Mid-gynoecium with massive central placentae; inner stamens freed. I) Mid-gynoecium showing the three freed septal wings with marginal papillae and the branched funicular network; ovules not shown. J) Upper gynoecium with only the septal axials (SA) present. K) Upper gynoecium showing a given dorsal (D) in three positions due to its looped course; no ventral vasculature evident. L) Upper depressed gynoecium surrounding the three freed styles; locules closing. M) Three free styles above the gynoecium each lined with stigmatoid tissue.

HELONIAS BULLATA**E****I****M****D****H****L****C****B****G****K****A****F****J**

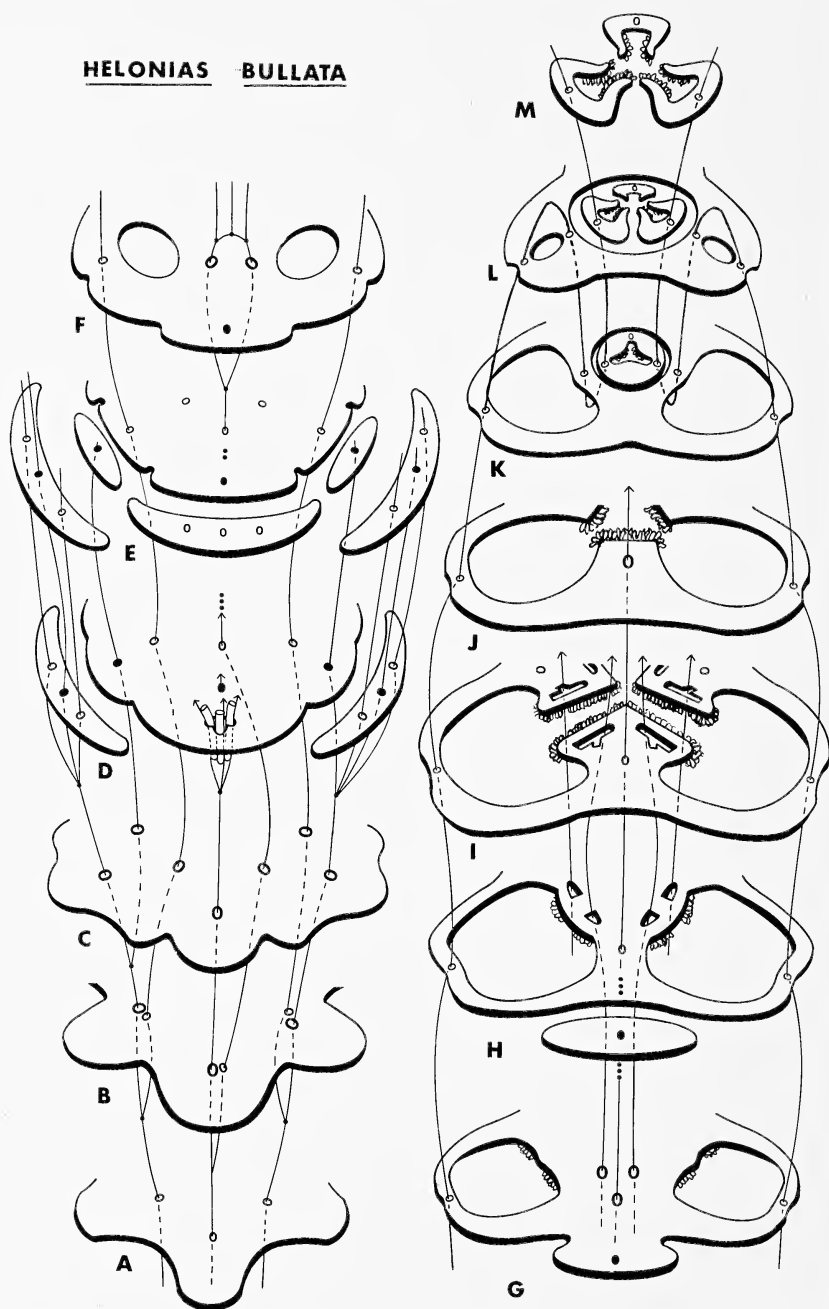
HELONIAS BULLATA

Fig. 6.—Projected cross-sections of *Helonias bullata*. Lettered sections correspond to those of Fig. 5.

ascent. Yet their overall path is most remarkable (Figs. 4C–F, 5G–K, 6G–K, 7). Cross-sections through the upper ovary and style reveal a given dorsal in three places: in the outer carpellary wall where it has a normal arrangement of xylem and phloem; in the inner margin of the depressed carpellary wall where the bundle arrangement is reversed; in the freed style where the arrangement is again normal. Each dorsal (D) terminates in a free recurved style. In the upper ovary, there is no interconnection between the dorsals (D) and the ventral supply (Figs. 5–7). This unusual dorsal course parallels that observed in *Heloniopsis orientalis* (Utech and Kawano, 1977).

The three bundles which are to supply the ventral vasculature are found centrally as the locules open (Fig. 3A). These crescent-shaped bundles first divide radially to form the two major placental strands of that septum. Each septum has two such placental ventral strands (P_1 and P_2) (Figs. 3B–D, 5H–I, 6H–I). Side branches from these placental bundles form along the radii of their origin and fuse, thus closing the gaps formed between the placentals. These fusion bundles are the septal axials (SA) (Figs. 3B–D, 4A, 506). There is a single, fusion septal axial in each septum. The placental strands have a rotated (not a true reversed) xylem and phloem arrangement, whereas the septal axials have a normal arrangement. There is no terminal cross-connection between the septal axials and the other ventral bundles, though they all had a common basal origin. The placental strands (P_1 and P_2) depart laterally from the septal radii and move outward towards the septal wing-tip margins. The central gynoecium base is not subdivided at this level.

Each placental bundle (P_1 and P_2) establishes a funicular network along the septal wing-tip margin, and supplies half of the ovules in the adjoining locule. The funicular branches from the vertical placental strands are compound, and each supplies two ovules. Consequently, each septum has a zig-zag pattern of two rows of ovules on each side. Each locule, therefore, has four rows of ovules with two rows being supplied by adjacent septa (Figs. 3B–D, 5I–J, 6I–J, 7). The total (average) number of ovules per septum (locule) is usually 16 (Fig. 7, Table 1). The vertical placental strands end terminally in their respective septum without any cross-connection to the septal axials (SA) or dorsals (D) (Figs. 5–7).

General gynoecial morphology.—The gynoecium is unilocular terminally, tricarpellate, and nonstipitate. The dorsal and ventral supplies are independent and each is established basally before the tepals and the outer stamens are cut off. The fused central placenta has three independent ventral plexuses. From the middle of the upper region of the gynoecium, the central placenta is divided into three free septa (Figs. 3A–D, 5G–J, 6G–J). Ovule orientation is variable (heterotrophic). The outer pericarp wall is remarkably thin (chartaceous) at all stages,

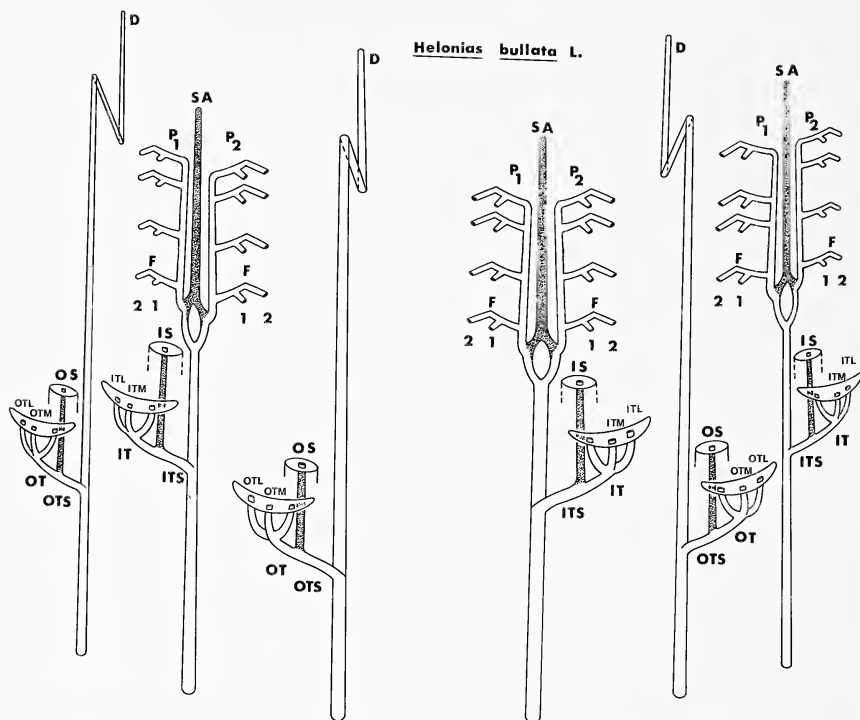


Fig. 7.—Summary longitudinal diagram for *Helonias bullata*; various bundles are coded: OTS = common outer tepal-stamen; OT = common outer tepal; OS = outer stamen; OTM = outer tepal median; OTL = outer tepal lateral; ITS = common inner tepal-stamen; IT = common inner tepal; IS = inner stamen; ITM = inner tepal median; ITL = inner tepal lateral; D = dorsal; $P_1 = P_2$ = vertical placental (ventral supply); F = funicular; SA = septal axial (fusion).

whereas, on the other hand, the basal central axis, the septal wings, and their associated inner margins are relatively thick in cross-section.

The ovary is broadly trilobed (Figs. 5, 6). There are no septal glands or indentations, because there is complete lateral fusion between the septal wings. Raphides are present, but rare, in the septal wings, only at maturity. A dorsal notch or groove is present at all cross-sectional levels from the ovary base to the region of style origin (Figs. 5, 6). This carpellary indication of loculicidal dehiscence is confirmed in the mature fruits. Occasionally, irregular tears are observed in the upper, outer septal region, but this should not be interpreted as septicidal dehiscence. There is considerable mechanical pressure in this zone at maturity from the tight ranking of the appendaged seeds.

Both in bud and early flower, the bottoms and upper, extended lobes

of each locule are empty, but in fruit the locules are filled by the elongated appendages of the seeds. In fruit, the tightly appressed seeds are so arranged that their free ends are directed into the free upper locular spaces.

The free and recurved styles are lined by nonpapilloid stigmatoid tissue (Figs. 4D–F, 5J–K, 6J–K), though this cell type is replaced in the upper ovary by more elongated papilloid cells. This latter cell type extends downwards in each locule along the free septa's inner margins (Figs. 3B–D, 5D–I, 6D–I).

The three upper carpellary lobes of the flowering gynoecium are greatly expanded in fruit. The dorsals (D) and their associated dorsal grooves pass over the crests of these lobes. Loculicidal dehiscence along the dorsal grooves is the rule. The internal locular spaces within these lobes are occupied by the free, elongate, and upturned appendages of the seeds. There is no vascularization, excluding the dorsals (D), in the outer, thin, chartaceous carpellary walls.

Comparison of Helonias bullata and Heloniopsis orientalis

In completing the vascular floral anatomy and carpel morphology of *Helonias bullata*, begun by Anderson (1940), certain salient features are noteworthy. The preliminary observations of Anderson were correct and indeed they do represent a peculiar floral type within the subfamily Melanthiodideae. They are not, however, unique as will be shown in the following comparison to the Asian *Heloniopsis orientalis*.

In Asa Gray's classical paper (1859) on the relations of the Japanese flora to that of North America and other parts of the northern temperate zone, he also created the genus *Heloniopsis*. In the related discussion for this genus, he stated that this species may be briefly described as a *Helonias* with few flowers, a single and slender style surmounted by a depressed-capitate stigma, and the seeds appendaged only at the hilum. The last character only is true for immature seeds. The similarity of the two species has been clear from the inception of *Heloniopsis* (meaning like *Helonias*), but subsequent workers have separated them into different liliaceous tribes, for example Hutchinson (1934, 1959).

Table 1 is a summary of both vegetative and floral characters of *Helonias bullata* and *Heloniopsis orientalis*. *Heloniopsis orientalis* (Thunb). C. Tanka *sensu lato* (including *H. pauciflora* A. Gray, *H. japonica* Maxim., *H. grandiflora* Fr., and Sav., and *H. breviscapa* Maxim.) and its varieties (var. *flavida* (Nakai) Ohwi and var. *breviscapa* (Maxim.) Ohwi) extend southward from Sakhalin Island and Korea through the Japanese Islands of Hokkaido, Honshu, Shikoku, and Kyushu, where rare (Ohwi, 1965; Kitamura et al., 1975). Although *H.*

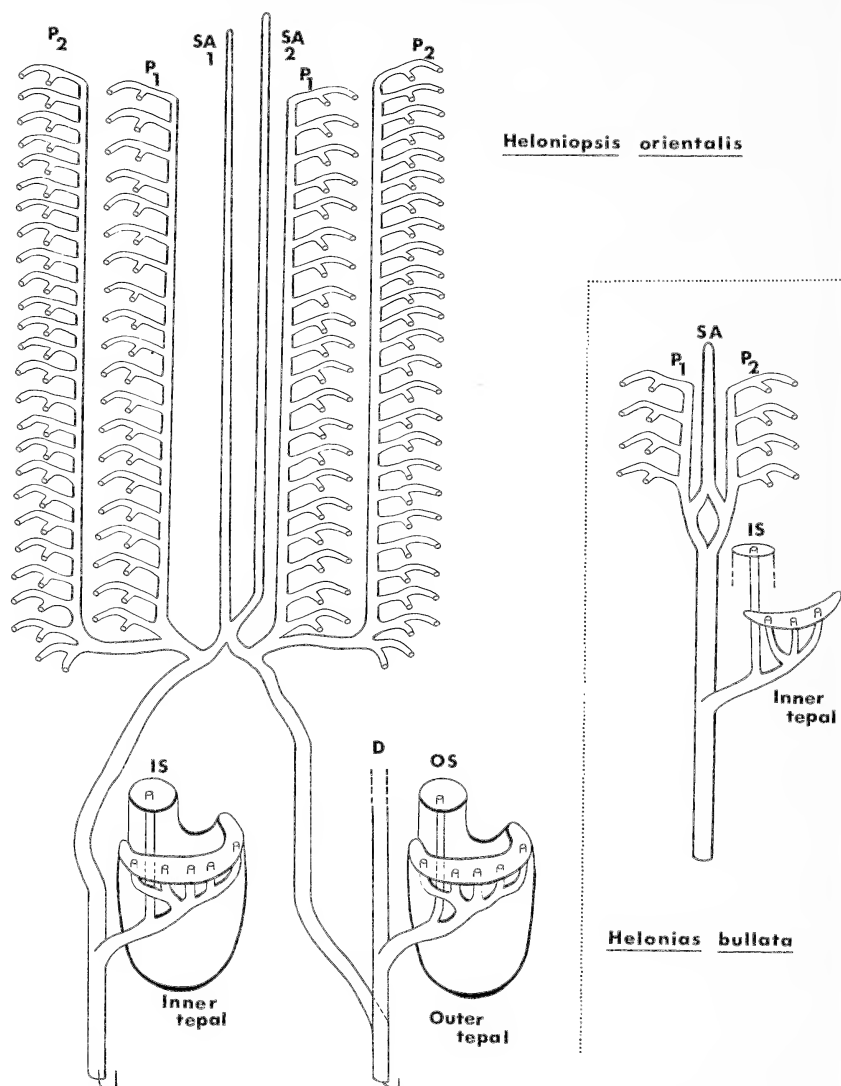


Fig. 8.—Comparison of the ventral vasculature of *Heloniopsis orientalis* (Utech and Kawano, 1978; in part) and *Helonias bullata*. *Heloniopsis* is based on an average of 180 ovules (seeds) per septum; *Helonias*, on an average of 16 ovules (seeds) per septum. Bundles coded as in Fig. 7.

orientalis is more common northward, it has a broad ecological amplitude in Japan and occurs in lowland evergreen forests, and at times in alpine gardens. Although the American *Helonias bullata* is rarer than the Asian *Heloniopsis orientalis*, the former also exhibits a par-

allel elevational spectrum, that is, it occurs in the southern Blue Ridge Mountains and northward shifts to the lower coastal plains (Fig. 1). Both species have warm temperate affinities (Ohwi, 1965; Numata, 1974; Wood, 1970; Hara, 1958, 1959) and are part of the old Arcto-Tertiary Geoflora assemblage (Li, 1971; Good, 1964; Tanai, 1972; Graham, 1972).

The gross morphological and anatomical differences between *Helonias bullata* and *Heloniopsis orientalis* can be effectively compared and understood from a reproductive point of view. Both species have similar methods of vegetative reproduction, although their detailed sexual reproductive patterns differ significantly. If one compares these patterns and the net seed production of the two, the apparent differences are minimal.

The average number of seeds produced for each species can be estimated as follows: *Helonias bullata*—16 ovules (or seeds)/carpel \times three carpels/flower \times 51.3 flowers/inflorescence = 2462.4 ovules (or seeds)/inflorescence; *Heloniopsis orientalis*—180 ovules (or seeds)/carpel \times three carpels/flower \times 4.7 flowers/inflorescence = 2538.0 ovules (or seeds)/inflorescence. Seed set is high in both species. This preliminary estimate of the numbers of ovules or seeds produced for the two species is almost the same, even though their flower and ovule numbers differ significantly (Table 1).

It would be interesting to speculate about the sexual reproductive capacity of a hypothetical common ancestor(s), which most certainly belonged to the Arcto-Tertiary Geoflora. Because there are no fossil records for these two species, I would predict that their ancestor(s) had a similar net seed production as the two today. The evolutionary divergence that occurred between *Helonias* and *Heloniopsis* followed different reproductive paths, yet the base level of seed production has remained the same. The fewer, but larger flowers in *Heloniopsis* have deep, saccate tepal nectaries, which promote both outbreeding and a high constancy in seed set. The floral geometry of this species with its long style and widely divergent filaments also promotes outbreeding (Table 1; Utech and Kawano, 1978). *Helonias*, on the other hand, has many closely spaced, small flowers. There are no tepal nectaries in this species. The short, recurved styles in relation to the pollen dispersal zone (Table 1), as well as the close interfloral spacing, would suggest a higher probability of inbreeding.

The ventral network is the chief vascular difference between the two species. Fig. 8 diagrams these ventral networks. *Heloniopsis* has on the average 180 ovules per septum, whereas *Helonias* has only 16 ovules per septum. Within a given septal margin of *Heloniopsis* there are eight-ranked rows of ovules with the same number of funicular traces, whereas there are only four-ranked ovule rows in *Helonias*.

The mature seeds of *Heloniopsis*, beside being more numerous per carpel than those in *Helonias*, are also longer (Table 1). Initially the vasculature underlying this gross morphological difference appears extreme (Fig. 8), but upon closer examination the respective vasculatures are really variations on the same theme.

In *Helonias bullata*, the ventral supply of each septum is established by a single gynoecial base bundle with normally arranged xylem and phloem. There are three such basal bundles per gynoecium. Although they are compound, as shown by later subdivisions (Figs. 5–7), they have not had a fusion origin. Subsequently, each bundle divides within its septum to form a septal axial (SA) and two vertically ascending ventral placentals (P_1 and P_2) (Figs. 5–8). The placentals rotate slightly towards the septal margins to supply the ovules via compound funicular branches. The placentals, like the septal axial of a shared septum, have a normal xylem and phloem arrangement. The septal axials (SA), it should be noted, are fusion products. The branched funicular traces (F), which arise in ranks from the two placentals (P_1 and P_2), establish the four-rowed ovule arrangement. Terminally there is no cross-connection between the septal axials and the associated placentals.

In *Heloniopsis orientalis*, on the other hand, the ventral vasculature of each septum has several additional modifications (Fig. 8). At the base of the gynoecium, in addition to the three dorsals, there are three pairs of additional bundles. Each pair is along a septal radius and each member has normally disposed conducting elements. In *Helonias*, there had only been a single bundle in a similar position. One bundle of the pair is a continuation of the pedicel bundle that supplied an inner stamen and inner tepal, whereas the other member of the pair is a continuing radial branch from an adjacent pedicle bundle which continued as the dorsal after supplying an outer stamen and outer tepal.

Within each septum, a fusion occurs between radial branches from the two original septal pair members. This fusion bundle divides to form two septal axials (SA₁ and SA₂). The outermost of the two (SA₁) has normally arranged xylem and phloem, whereas the inner one (SA₂) has a reversed pattern (Fig. 8). Again both septal axials are fusion products.

Concurrent with the double septal axial formation, each main branch of the original septal pair undergoes a radial division to form two ascending placental strands (P_1 and P_2 and P_1 and P_2) (Fig. 8; Utech and Kawano, 1977). Those placental bundles furthest from the central axis, the two P_1 , have a normal conducting element arrangement, whereas those two nearest the center, the two P_2 , have a reversed arrangement. Each septum consequently has three outer bundles with normally ar-

ranged conducting elements, that is P_1 , SA_1 , and P_1 , and three inner bundles with reversed elements, that is P_2 , SA_2 , and P_2 (Fig. 8).

CONCLUSION

The total vascular floral anatomy of *Helonias bullata* is derived from six free pedicel bundles. Through a series of radial divisions, but not fusions, three of the pedicel bundles establish the outer tepal, outer stamen, and dorsal vasculature. The three remaining and alternating bundles of the pedicel configuration establish the inner tepal, inner stamen, and ventral vasculature. There is no cross-fusion between the dorsal and ventral supply networks. The ventral network of each septum involves a fusion septal axial, two vertical placentals and a compound, branching funicular bundle that supplies ovules in four-ranked rows. Two rows occur on each side of the septum.

The gynoecium is unilocular terminally, tricarpellate, and nonstipitate. Neither septal glands nor septal indentations are present, but dorsal grooves, which indicate the lines of locucidal dehiscence, occur. Raphides are present, but rare, and only at maturity. The three recurved styles are depressed into the upper ovary. The three locule lobes are extended at maturity to accommodate the distal ends of the appendaged seeds.

Besides the numerous vegetative similarities and a common chromosomal base number ($2n = 34$) shared by *Helonias* and *Heloniopsis*, their basic vascular floral anatomies are similar. The patterns of origins for the tepal, stamen, and dorsal bundles are identical. The dorsals in both species follow a similar looped course over the locule lobes. The ventral supplies do differ, but they are based on the same theme. The net ovule (or seed) production per inflorescence, which is also similar, can be related to the different flower sizes and the different number of flowers per inflorescence, as well as to a hypothetical Arcto-Tertiary Geoflora ancestor.

Based on the similarities between *Helonias* and *Heloniopsis*, the tribal association of the two in the Helonieae should be maintained. One might even argue for congeneric status for the two, that is, in *Helonias*.

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A NEW GENUS AND SPECIES OF PHYLLOTINE RODENT (MAMMALIA: MURIDAE) FROM NORTHWESTERN ARGENTINA

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ABSTRACT

Andalgalomys, a new (Recent) genus of phyllotine rodent is described. Included species are *A. olrogi*, a new species from the *Larrea* desert of the Bolsón de Pipanaco, Catamarca Province, Argentina, and *A. pearsoni* (Myers), which is reassigned from the genus *Graomys*. *Andalgalomys* is considered to be most closely related to *Calomys* and *Eligmodontia*, and is somewhat intermediate to *Calomys* and *Graomys* in a linear arrangement. Dental and cranial features of *Andalgalomys* are especially close to *Calomys*, with *A. pearsoni* exhibiting more primitive features and a closer similarity to *Calomys* than *A. olrogi*. *A. pearsoni* is considered to be quite similar to a generalized Chacoan ancestral form, and lives today in intersylvan grassland refugia in the Paraguayan Chaco. *A. olrogi* is specialized for a desert habitat, exhibiting bullar enlargement, lateral digit reduction, and lengthening of its appendages. The karyotype of *A. olrogi* consists of a $2n$ of 60, with 116 autosomal arms. The X-chromosome is a large submetacentric, and the Y is a small submetacentric. This karyotype is the most divergent among the phyllotines, but can be derived from that of *Calomys sorellus* by pericentric inversions.

INTRODUCTION

Phyllotine rodents are a South American group of primarily pastoral cricetines, which are allied in an informal, but seemingly natural

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grouping of from seven (Hershkovitz, 1962) to eleven (Pearson and Patton, 1975) or more genera. The phyllotines are better known taxonomically than other South American cricetines, the species of the group having been reviewed by Hershkovitz (1962). Additionally, Pearson's (1958) revision of the genus *Phyllotis*, and Pearson and Patton's (1975) report on the karyology of phyllotines have added greatly to our understanding of the relationships of the phyllotine genera. Although much remains to be learned about the systematics of phyllotines, the group composition and intragroup interspecific relationships are becoming increasingly clear. In this paper, we follow the clustering of Sigmodontini species as set forth by Pearson and Patton (1976) and Gardner and Patton (1976).

Phyllotines are included within the tribe Sigmodontini, subfamily Cricetinae, of the family Muridae (Hershkovitz, 1966). The phyllotine species have complex penes, with the distal cartilagenous portion of the bacula being tridigitate. Penis and baculum morphologies among phyllotines are quite diverse, and the differences between phyllotine genera are as great as the differences among the Sigmodontini groups with complex penes (that is, the akodonts, oryzomyines, phyllotines, and sigmodonts, Hooper and Musser, 1964). The Sigmodontini form an adaptive complex that encompasses aquatic, subfossorial (including the adaptively similar grass-tunneling voles), scansorial, and arboreal species. Overall, these four groups are little differentiated morphologically, and both intragroup and intergroup parallelism and convergence are common. Furthermore, some apparently annectent forms between groups and between genera within groups compound the difficulties of arranging a satisfactory taxonomy.

Phyllotines are most diverse in grasslands, scrublands, deserts, and arid Andean highlands. They occupy semitropical deciduous forests, and are uncommon in palustrine habitats. The majority of species are scansorial, some are vole-like in habits and appearance, and a few (for example, *Graomys*) are somewhat arboreal (Mares, 1973, 1976). Overall, phyllotine species richness is low in lowland desert and semidesert habitats, and most species are associated with rock-scrub habitats of upper bajadas or xeric montane ecosystems. *Eligmodontia typus* and *Phyllotis gerbillus* are the most desert-adapted phyllotine species. The former is widespread in dry steppe, desert, and puna habitats in the Andes and intermountain valleys of Argentina, Chile, and Bolivia, and in southern Peru. The latter is apparently confined to the Sechura Desert of northwestern Peru (Hershkovitz, 1962; Mares, 1973; Pearson, 1972). *E. typus* has the most pronounced morphological adaptations to a desert habitat, possessing spade-shaped, gerbil-like hind feet, with single, large, hirsute cushions on the soles (Hershkovitz, 1962). However, the external pinnae and auditory bullae are only moderately

enlarged, and are less noteworthy than those of the rock and scrub inhabitants, *P. amicus*, *P. boliviensis*, and *Graomys griseoflavus*. Both lowland desert species are fairly well-adapted, physiologically, to desert life (Koford, 1968; Mares, 1975, 1977a).

It surprised one of us (Mares), during field studies in the desert of Catamarca Province, Argentina, to discover that a mouse just removed from a livetrapped (and presumed to be *E. typus*) had no hairy pads on the hind feet. Unfortunately, this discovery came during actions ancillary to specimen preparation, and although it was presumed at that time to be a new species, three and one-half years elapsed before four additional specimens were captured and chromosome data were secured. Examination and comparison of the five specimens with all other remotely similar South American rodents convinced us that this form had no known close relatives, but was allied with the phyllotines. Superficially, the specimens are very similar to the sympatric *E. typus*. However, they differ in numerous details, most notably in their naked-soled, cushionless feet, greatly inflated auditory bullae, and their different molar cusp patterns. Most surprising, however, is the striking similarity of these specimens in external and cranial details to some of the Old World gerbillines.

Subsequent to the discovery of this new form, and prior to its description here, Myers (1977) described a new species of phyllotine (*Graomys pearsoni*) from the dry grassland islands in the Chaco of western Paraguay. Our analyses lead us to the conclusion that *G. pearsoni* and the new species from Catamarca Province, Argentina, are most closely related and together comprise a new genus.

METHODS

Somatic chromosomes of bone marrow cells were prepared using the colchicine, hypotonic sodium-citrate technique of Patton (1967). Karyological nomenclature is as defined by Patton (1967). The specimens examined cytologically are listed in the description of the new species.

Phalli were prepared using the techniques outlined by Lidicker (1968). However, 6 to 8 h were sufficient for clearing the dry phalli in 2% KOH, and a day's stay (as little as 12 h) resulted in disintegration of the soft tissues. Also, a few drops of 2% KOH, added to the alizarin solution, hastened the staining of the osseous material. Terminology and measurements of phalli are as defined by Hooper and Musser (1964).

Fifty-one dental characters were evaluated qualitatively for each specimen of the new genus, and for five specimens each of *Calomys callosus*, *Eligmodontia typus*, and *Graomys griseoflavus* (see list of specimens examined). Also, the same characters were evaluated for at least one each of the other species listed in the "specimens examined." These dental traits are primarily those utilized by Hershkovitz (1962) in defining the genera and species of phyllotines. Those, and others found useful by us in distinguishing genera and species, are presented in the formal descriptions and, unless otherwise indicated, are as defined by Hershkovitz (1962). In addition, thirty-nine external and cranial traits were measured. These morphometric characters are listed in Table 1, and are as illustrated by Hershkovitz (1962) or defined by DeBlase and Martin (1974), except for the following.

Interparietal length.—Greatest length of the interparietal bones, measured at, or near, the midpoint on the cranium.

Rostral width.—Greatest width across the rostrum at a point immediately anterior to the zygomatic processes.

Incisive foramen length.—Greatest length of the incisive foramen; where the two foramina were asymmetrical, the longer of the two was measured.

Distance between molar rows.—Least distance between the upper molar rows, measured from the lingual sides of the molars.

Parapterygoid fossa width.—Width across the parapterygoid fossa, measured from the outer edge of the pterygoid process to the outer rim of the parapterygoid fossa. This measurement was taken at the midpoint of the fossa.

Mesopterygoid fossa width.—Width between the pterygoid processes, measured in the same plane as the parapterygoid fossa width.

Number of palatal foramina.—A count of the foramina on the palate between, and including, the posterior palatal foramen and the anterior palatal foramen. In most species, the numbers differ on the right and left sides, so the two sides were scored separately.

Incisive foramen intrusion.—The anterior-posterior distance that the incisive foramina extend between the molar rows.

Length of molars.—The greatest length of each of the molars, measured from occlusal view. In species with molars that are excessively tilted in an anterior-posterior plane, the first upper molar was measured from labial view.

Univariate statistical analyses included standard statistics and Student's *t*-tests of samples of the new genus. Multivariate analyses were performed using a stepwise discriminant function program (BMD07M, Dixon, 1976) and numerical taxonomic programs (MINT). The discriminant function program performs multiple group discriminant analyses, utilizing linear classification functions. Squared Mahalanobis distance statistics (D^2) and canonical analysis are also included in this program. Average Euclidean distance (taxonomic distance) coefficients, and Q-mode correlation (similarity) coefficients were calculated using the MINT programs. Data were standardized in the MINT programs, and phenograms were constructed by the unweighted pair-group method using arithmetic averages.

SPECIMENS EXAMINED

All specimens used in the morphometric analyses were young adults or older. In addition to the specimens that were used in the multivariate and/or qualitative analyses and which are listed below or beyond, hundreds of specimens, representing most South American cricetine species, and including all of the *Graomys* holotypes (but excluding *G. pearsoni*), were examined and compared with the new form. All of the specimens listed are preserved as standard skin and skull preparations, and are deposited in the Carnegie Museum of Natural History (CM) unless they are designated as being housed elsewhere. Specimens with the acronym AMNH are in the American Museum of Natural History, and those designated UCONN are deposited in the University of Connecticut Museum of Natural History. The initials BM designate the British Museum of Natural History.

Akodon varius Thomas.—ARGENTINA. *Tucumán*: Horco Molle, 20 km NW San Miguel de Tucumán (5).

Aodinomys edax Thomas.—ARGENTINA. *Tucumán*: Horco Molle, 15 km W San Miguel de Tucumán (3).

Auliscomys sublimis Thomas.—ARGENTINA. *Salta*: along Highway 40, S of junction of Highways 40 and 51, 4,100 m (1).

Calomys callosus (Rengger).—ARGENTINA. *Tucumán*: Horco Molle, 25 km NW San

Miguel de Tucumán (1); Quebrada de Lules (below dam), 8 km SW San Pablo (4).

Calomys muriculus (Thomas).—BOLIVIA. *Santa Cruz*: Santa Cruz de la Sierra (1); Puerto Suarez (1).

Calomys musculus (Thomas).—ARGENTINA. *Catamarca*: 10 km (by road on Route 62) W Andalgalá (1).

Eligmodontia typus Cuvier.—ARGENTINA. *Catamarca*: 1.5 km S Andalgalá (1); 6 km N Saujil (1). *Mendoza*: 31 km W (by El Manzano Rd) of Tunuyán (2). *Tucumán*: 45 km S Cafayate, along Highway 40 (1).

Graomys edithae Thomas.—ARGENTINA. *Catamarca*: Otro Cerro, about 18 km NNW Chumbicha (1), BM.

Graomys domorum (Thomas).—ARGENTINA. *Salta*: 11 km N Anta (1). BOLIVIA. *Cochabamba*: Parotani, 8,800 ft (4), AMNH.

Graomys griseoflavus (Waterhouse).—ARGENTINA. *Catamarca*: Rio Andalgalá, immediately N Andalgalá (5). BOLIVIA. *Santa Cruz*: Campos de Guanacos (5).

Holochilus brasiliensis (Desmarest).—ARGENTINA. *Formosa*: Estancia Santa Catalina, approximately 5 km W Cogoy, Departamento de Patiño (1).

Oryzomys albigularis (Tomes).—COLOMBIA. *Magdalena*: Sierra del Libano (1). *Santander*: Peña Blanca (1). BOLIVIA. *Cochabamba*: Incachaca (2).

Oryzomys capito (Olfers).—ARGENTINA. *Salta*: 24 km NW Agua Blanca, Departamento Orán (1).

Oryzomys longicaudatus (Bennett).—ARGENTINA. *Catamarca*: Rio Andalgalá, immediately N Andalgalá (4); La Toma, 6.5 mi N Andalgalá (1).

Oxymycteris parasilensis Thomas.—ARGENTINA. *Salta*: 24 km NW Agua Blanca, Departamento Orán (1).

Phyllotis darwini (Waterhouse).—ARGENTINA. *Catamarca*: along Rio Potrero, 10 km (by road) N Potrero (1); Hills at E end of La Puntilla (2). *Cordoba*: La Cumbre, en Estancia de la Loma, approximately 1 km from Estancia el Rosario (1). *Tucumán*: Horco Molle, 15 km W San Miguel de Tucumán (1).

Phyllotis micropus (Waterhouse).—CHILE. *Llanquihue*: Rio Nireguao (1).

Phyllotis osilae J. A. Allen.—ARGENTINA. *Tucumán*: El Infiernillo, 18 km NW (by road) Tañ del Valle (2); El Infiernillo, 19 km NW (by road) Tañ del Valle (1).

Reithrodon physodes (Olfers).—CHILE. *Llanquihue*: Rio Nireguao (1).

Zygodontomys lasiurus Thomas.—BRAZIL. *Pernambuco*: Exu (1).

DESCRIPTIONS

Andalgalomys, new genus

Type species.—*Andalgalomys olrogi*, new species.

Included species.—*Andalgalomys olrogi*, new species; *Andalgalomys pearsoni* (Myers).

Diagnosis.—A member of the tribe Sigmodontini, subfamily Crice-tinae, of the family Muridae; most closely allied with the phyllotine species. Size moderately small, with slightly to moderately haired and pencilled tail; tail longer than head-body length; pinnae moderately large and sparsely covered with fine hairs; soles of feet naked. Skull with divergent (posteriorly) interorbital region; supraorbital region ledged; nasals slender and straight; molar rows parallel; palatines with large slits usually present; parapterygoid fossa border ledged anteriorly and medially; bullae relatively greatly inflated. Molars brachydont, their crowns tuberculate and slightly crested, with some tendency to-

ward lamination in the upper molars. M^1 with well-developed anterior median fold and an anteromedian style; postcingulum with a slight notch or fold. M^2 anteroloph small, and directed nearly anterior. Major fold of M^3 deep, dividing the metacone-hypocone from the protocone-paracone by a double enamel wall that usually persists in worn teeth. Procingulum of M_2 not evident, and anteroconulid not apparent. Baculum tridigitate, the medial digit shorter than the lateral digits, and curved slightly dorsad; lateral digits robust; proximal end of baculum expanded laterally, and straight edged; distal end slightly expanded and ball-shaped; bacular mounds extend beyond glans hood. Glans penis as long as, or longer than, baculum.

Etymology.—This genus is named for the village of Andalgá, near which the type species was captured, and of which the authors have fond memories.

Description.—Size moderately small (see Table 1). Tail longer than head-body length, and sparsely to moderately haired, the hairs at the tip forming a very slight (<3 mm beyond tip) to moderate (5–9 mm) pencil. Ear pinnae well developed and sparsely haired. Pelage of moderate length (hairs on rump 5–10 mm) and of soft texture. Feet with naked soles; hind feet with six plantar tubercles (Fig. 4); first hind digit small, not, or barely (claw tip only) reaching the base of the second digit; hind digits 2 to 4 somewhat elongated.

Skull with moderately inflated braincase, slightly narrower than the zygomatic width. Interparietals broad, extending the width of the dorsal cranial surface; their length short. Sides of supraorbital region with overhanging ledges that extend as ridges onto the temporal region; interorbital region moderately constricted, being about the same width as the rostral width; interorbital region evenly divergent posteriorly (wedge shaped). Zygomatic arches only slightly convergent anteriorly; the anterior border of the zygomatic plate slightly concave. Premaxillae barely encroaching on the dorsal surface of the rostrum, except at the premaxilla-frontal suture. Nasals straight, not noticeably divergent or convergent anteriorly, and relatively narrow; nasals concave, forming a shallow, longitudinal depression dorsally. Infraorbital foramen deeply notched dorsally. Incisive foramina narrow and extending to about the level of the first molars. Palate long and of moderate width; anterior palatal foramen coalesced with other palatine foramina to form a long slit (or infrequently present as small, independent foramina of variable number). Bullae greatly inflated compared to other phyllotines. Parapterygoid fossa width more than twice as great as the mesopterygoid fossa width, measured in the same plane; fossa moderately deep; anterior and medial borders of the parapterygoid fossa with a prominent shelf or ledge. Posterior border of mandible deeply notched; coronoid process small; condyloid process narrower than, or equal to, the greatest width of the angular process.

Upper incisors slender, opisthodont, their anterior faces smooth; upper molar rows parallel-sided, somewhat bowed outwardly medially; molars brachydont, their cusps tuberculate and crowns slightly crested; anterior enamel walls of upper molars slightly more projecting than the posterior enamel walls, both inclined posteriorly and somewhat rotated inwardly; the principal cusps of the outer side arranged either opposite or slightly in echelon to those of the inner side; upper molars with some tendency toward lamination, their cusps subovate to somewhat triangular in outline.

M^1 with well-developed anterior median fold, the procingulum bilobate, forming a larger anterolabial conule and a smaller anterolingual conule; anteromedian style on anterior surface of procingulum varies from obsolete (barely discernable) to well developed, but usually readily apparent; procingulum ovate in outline; postcingulum usu-

ally with a slight fold or notch; second secondary fold absent; mesostyle present or absent, when present, it is very tiny; anteroconule present or absent; anterolabial style present and well developed, or obsolete and represented only by a small shelf.

M² with small anteroloph directed nearly anterior; first primary fold shallow, but complete (not an island); second secondary fold absent; first minor fold small and directed in an anterior-posterior plane; postcingulum usually not apparent; metacone greater than or equal to hypocone in size; paracone greater than or equal to protocone in size; second internal fold complete (not an island).

M³ with an obsolete (rarely) or without an anteroloph; first primary fold obsolete (rarely) or absent; second secondary fold absent; major fold deep, usually completely dividing the protocone and paracone from the metacone and hypocone by a double enamel wall, even in moderate to well-worn teeth; postcingulum not evident.

M₁ with well-developed procingulum; anterior median fold forming a shallow notch (or rarely a deep groove) on the anterior surface of the procingulum, but also penetrating deeply as an enamel fold; second primary fold present; second secondary fold absent; first minor fold present; anterolingual and anterolabial conulids usually not well differentiated from each other, and usually of nearly equal size; labial edge of anterolabial conulid does not extend to the anterior labial edge of the protoconid; protoconid nearly opposite the metaconid; hypoconid opposite or slightly behind entoconid.

M₂ procingulum obsolete or absent; first minor fold not evident; second primary fold usually well developed (rarely absent); posterolophid small to very small; anteroconulid absent, or rarely present as a small ridge or shelf.

M₃ subovate to subtriangular (with a rounded posterior apex) in outline from occlusal view; procingulum not evident; first minor fold not evident; first primary fold about midway on the tooth.

Baculum short or moderately long and tridigitate; the lateral digits longer and more robust than the medial digit; medial digit curved somewhat dorsad; baculum shorter than, to about as long as, the glans penis; basal sides of baculum concave dorsally and ventrally; baculum base more or less straight edged; distal end of baculum slightly enlarged and ball-shaped. Glans penis short and stubby to moderately long; exteriorly plain, with or without slight sulci dorsally and ventrally; bacular mounds smooth, and extending slightly above glans hood; hood variable in profile, being more or less straight, or sloped.

Karyotype, as far as known, consists of a diploid number of 60, with 116 autosomal arms; the X is a large submetacentric; the Y is a small submetacentric.

Comparisons.—Overall, *Andalgalomys* occupies a position intermediate to *Calomys* and *Eligmodontia* on the one hand, and *Graomys* on the other, being closer to the *Calomys-Eligmodontia* complex than to *Graomys*. In a linear arrangement, *Graomys* is somewhat intermediate between *Andalgalomys* and *Phyllotis* (*sensu stricto*). Externally, *Andalgalomys* is very similar to *Eligmodontia* in size, form, and coloration. It can be distinguished from *Eligmodontia* by its longer, more pencilled tail and its naked-soled, cushionless feet. Cranially, *Andalgalomys* differs from *Eligmodontia* by its somewhat larger skull; more wedge-shaped (less rounded) and ledged interorbital region; and its large palatine slits. Dentally, *Andalgalomys* differs from *Eligmodontia* in having upper molar cusps that are more ovate (less triangular) in outline. The M¹ of *Andalgalomys* has a well-developed anterior median fold (as opposed to shallow or obsolete fold); the anteromedian style is usually present on the procingulum of *Andalgalomys*, but is absent

in *Eligmodontia*; the postcingulum of *Andalgalomys* is notched but is unnotched in *Eligmodontia*. The anteroloph of M^2 is directed anteriorly in *Andalgalomys* and anterolabially in *Eligmodontia*. The paracone and protocone of M^3 is divided from the hypocone and metacone by a deep major fold in *Andalgalomys*, but *Eligmodontia* has only a shallow major fold that does not bisect the tooth; the size of the tooth is smaller in *Eligmodontia*, and it is more square in outline (*Andalgalomys* is triangular in outline). The procingulum of M_2 is evident as an anteroconulid in *Eligmodontia*, but is absent or obsolete in *Andalgalomys*; the posterolophid is better developed (larger) in *Eligmodontia*. The first primary fold of M_3 is far anterior on the side of the tooth in *Eligmodontia*, but is located about midway on the tooth in *Andalgalomys*.

Andalgalomys is most similar cranially to *Calomys* (that is, *C. callosus* and *C. muriculus*, to which the following comparisons directly apply). Externally, *Andalgalomys* is somewhat larger than *Calomys*, with a noticeably longer tail, and with large, non-volelike appendages. The ears are especially larger and broader. The skull of *Andalgalomys* differs from *Calomys* in having a more slender rostrum, including narrower nasals; the infraorbital foramen is larger in dorsal view; the bullae are much larger, and globular rather than tapered in shape; the upper tooththrows are parallel sided rather than slightly divergent anteriorly; the incisive foramina are narrower; the mesopterygoid fossa is narrower. Dentally, *Andalgalomys* and *Calomys* are most similar. *Andalgalomys* differs from *Calomys* in having an anteromedian style on the procingulum of M^1 , and a notch or fold on the postcingulum. The anteroloph of M^2 is directed anterolabially in *Calomys*, but anteriorly in *Andalgalomys*. The major fold of M^3 is shallow in *Calomys*, and unlike *Andalgalomys*, it does not bisect the tooth transversely by a complete enamel fold. The anterior median fold of M_1 is obsolete in *Calomys*, but well developed in *Andalgalomys*; unlike *Andalgalomys*, there is no notch on the postcingulum of *Calomys*; and the procingulum continues as a definite ridge onto the protoconid in *Calomys*. The procingulum of M_2 is not apparent in *Andalgalomys*, but is evident in *Calomys*.

Externally, *Andalgalomys* (especially *A. olrogi*) looks like a small *Graomys griseoflavus*. Compared to *Graomys*, the skull of *Andalgalomys* is smaller (but see remarks concerning *G. edithae*), with more wing-shaped (less triangular) interparietals; the palatines of *Graomys* are without slits; the parapterygoid fossa of *Andalgalomys* is relatively deeper and has a shelf on the anterior and medial borders. The upper molars of *Andalgalomys* are more brachydont, with more crested (not planed) occlusal surfaces; the cusps of *Andalgalomys* are more ovate (less triangulate), and are not as strongly laminated as in *Graomys*.

The procingulum of M^1 in *Graomys* is usually without an anterior fold (there may be a slight fold visible in unworn teeth), and has no anteromedial style. The anteroloph of M^2 is larger and directed more anterolabially in *Graomys*; the metacone and paracone are smaller than or equal to the hypocone and protocone in size in *Graomys*, but are larger than the hypocone and protocone in *Andalgalomys*. The anteroloph of M^3 usually is absent in *Andalgalomys*, but is present in *Graomys* (although of tiny size). The anterior median fold of M_1 is not apparent in *Graomys*; the labial edge of the anterolabial conulid extends to the anterolabial edge of the metaconid in *Graomys*, but does not approach the metaconid or protoconid in *Andalgalomys*; the protoconid is located much more posterior to the metaconid in *Graomys* than in *Andalgalomys*. The first minor fold of M_2 is present and moderately developed in *Graomys*, but is absent (or rarely obsolete) in *Andalgalomys*; the anteroconulid is present as a ridge in *Graomys*, but is absent or rarely represented by an obsolete ridge in *Andalgalomys*. M_3 of *Graomys* is strongly S-shaped and somewhat rectangular in outline, but is subtriangular and not S-shaped in *Andalgalomys*.

Andalgalomys is smaller than any of the *Phyllotis* species that approach its geographic range. It can be distinguished from most *Phyllotis* by its wedge-shaped (rather than rounded) interorbital region, its relatively longer rostrum, and its larger bullae. *Andalgalomys* is similar in size to *P. gerbillus*, but differs in its dental cusp patterns, in the features elaborated above, and in other details (Hershkovitz, 1962).

Remarks.—*Graomys edithae* Thomas is somewhat similar to *Andalgalomys olrogi*. Cabrera (1961) listed *edithae* in the synonymy of *G. griseoflavus medius* without comment. Our examination of the *G. edithae* holotype was made at a time when only one specimen of *A. olrogi* was available for direct comparison. That examination, and photographs of the skull and teeth of *edithae* in hand, lead us to the conclusion that *G. edithae* is not congeneric with *Andalgalomys*, nor conspecific with *G. griseoflavus*. Unfortunately, the molars of *edithae* are too worn to be of much use in making any specific determination.

Graomys hypogaeus Cabrera, from Corral Quemado, Catamarca, Argentina, is another named form that approaches the range of *Andalgalomys olrogi*, and which, from its description (Cabrera, 1934), appears to be similar in size and form to *Andalgalomys*. Cabrera later (1961) synonymized *G. hypogaeus* with *G. g. medius*. A cursory examination of the holotype convinced one of us (Mares) that *hypogaeus* is an old, and rather large *Eligmodontia typus*. We have been unable to measure or thoroughly examine the holotype, but photographs at hand, kindly provided by E. Massoia, and an analysis of Cabrera's measurements (1934) reconfirm our conclusions that *G. hypogaeus* is an *Eligmodontia typus* (see discussion).

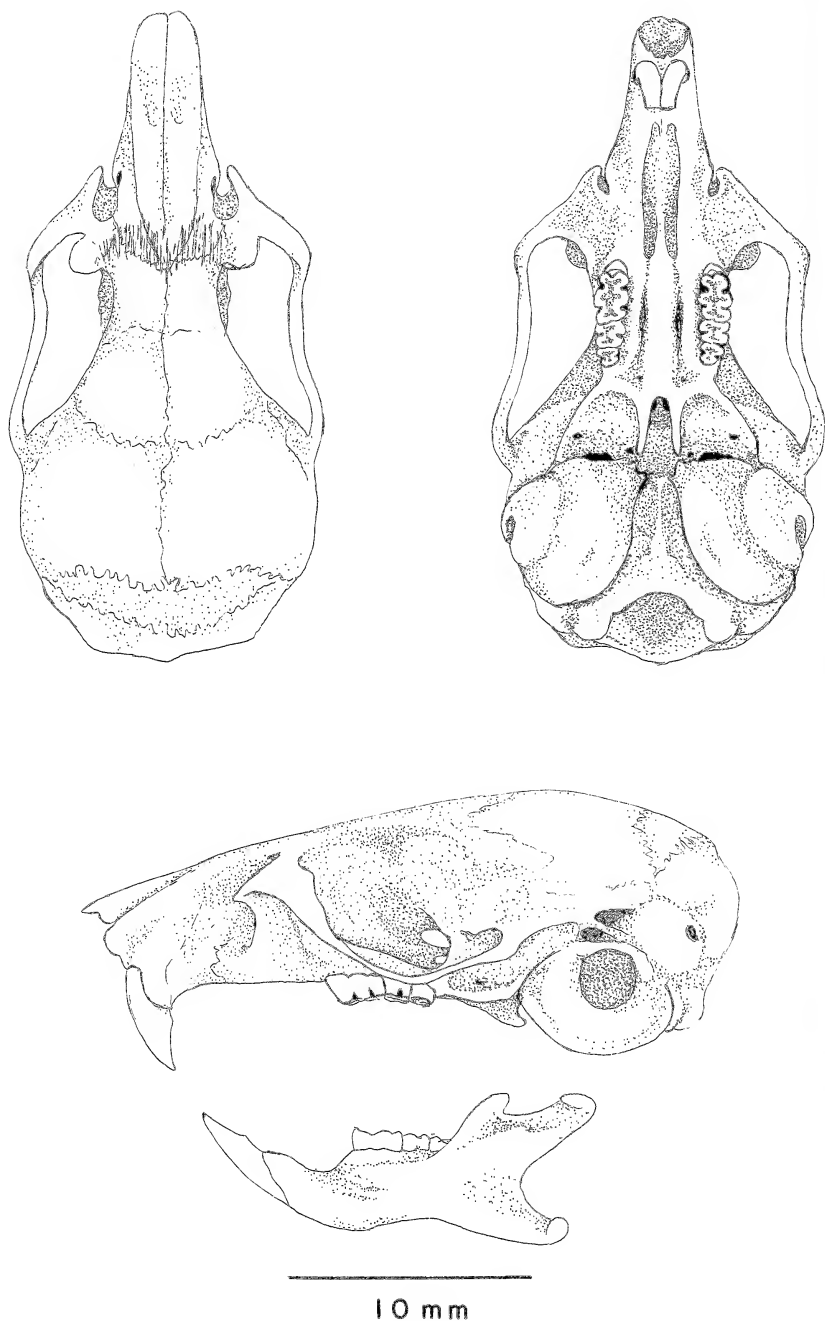


Fig. 1.—Skull of *Andalgalomys otrogi* holotype (CM 44024).

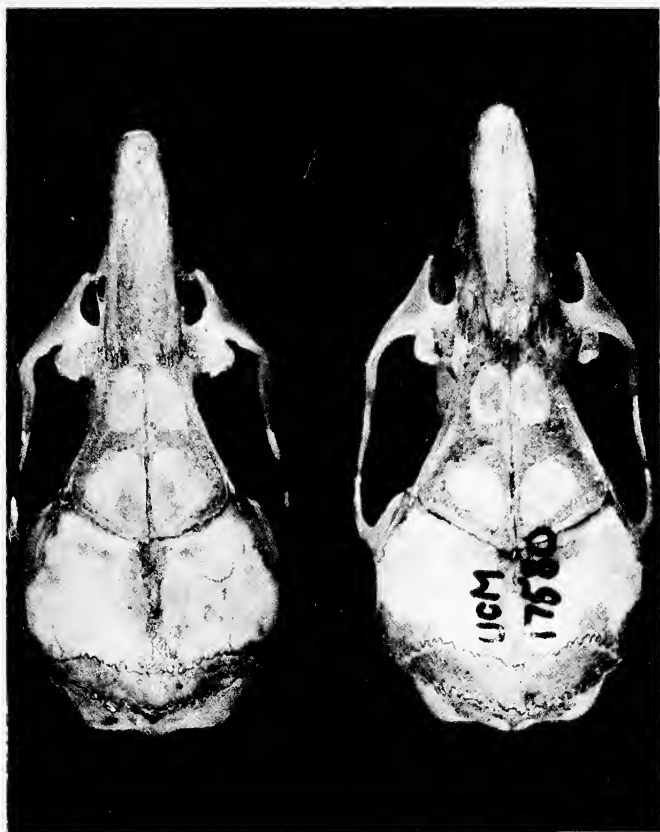


Fig. 2.—Dorsal view of skulls of mature specimens of *Andalgalomys*. Left, *A. olrogi* (CM 44023); right, *A. pearsoni* (UCONN 17580).

Andalgalomys olrogi, new species

Holotype.—Young adult female; skin, skull, and chromosomes, CM 44024; from West Bank Rio Amanao, about 15 km W (by road) Andalgalá, Catamarca Province, Argentina; obtained 19 January 1976 by D. F. Williams, original No. 2077.

Distribution.—Known only from three localities in the vicinity of the Rio Amanao, westward from Andalgalá in central Catamarca. Approximate elevation at the three localities is 950 m.

Diagnosis.—A moderately small, yellowish-brown mouse with a small whitish subauricular spot and a small, whitish postauricular patch; tail relatively long and moderately pencilled; pinnae large and

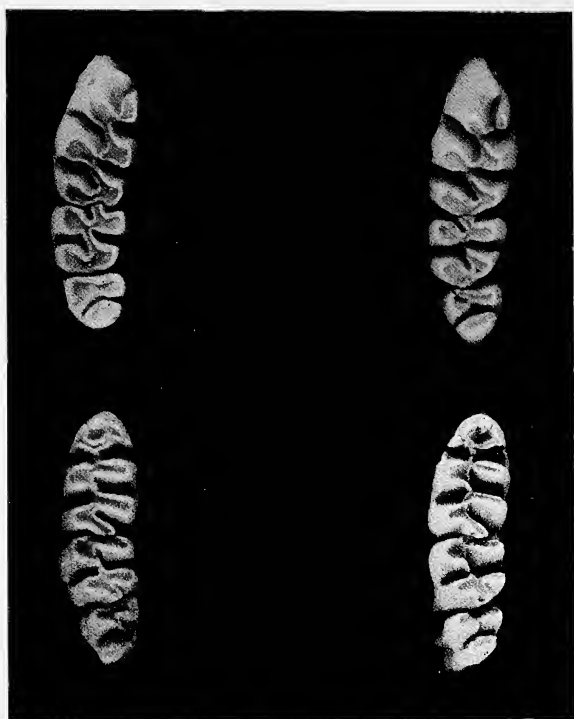


Fig. 3.—Upper and lower molar rows of *Andalgalomys*. Left, *A. olrogi* holotype (CM 44024); right, *A. pearsoni* (UCONN 17566). The molars of *A. olrogi* are slightly more worn than those of *A. pearsoni*. The teeth are coated with a layer of ammonium-chloride dust in order to reduce glare and to highlight the cusps and enamel folds.

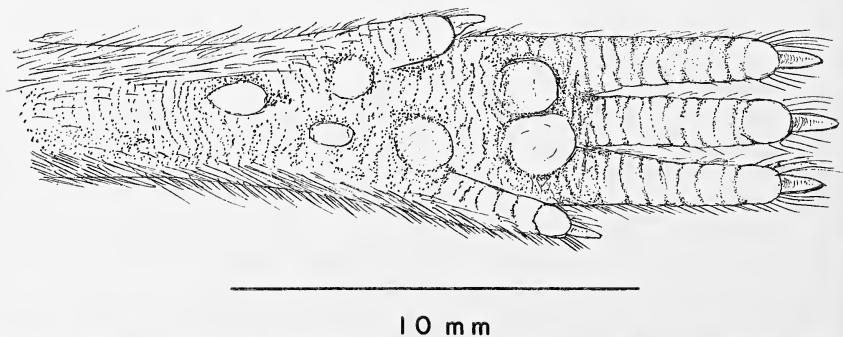


Fig. 4.—Left hind foot of *A. olrogi*. The drawing is a composite, based largely upon photographs of fresh material.

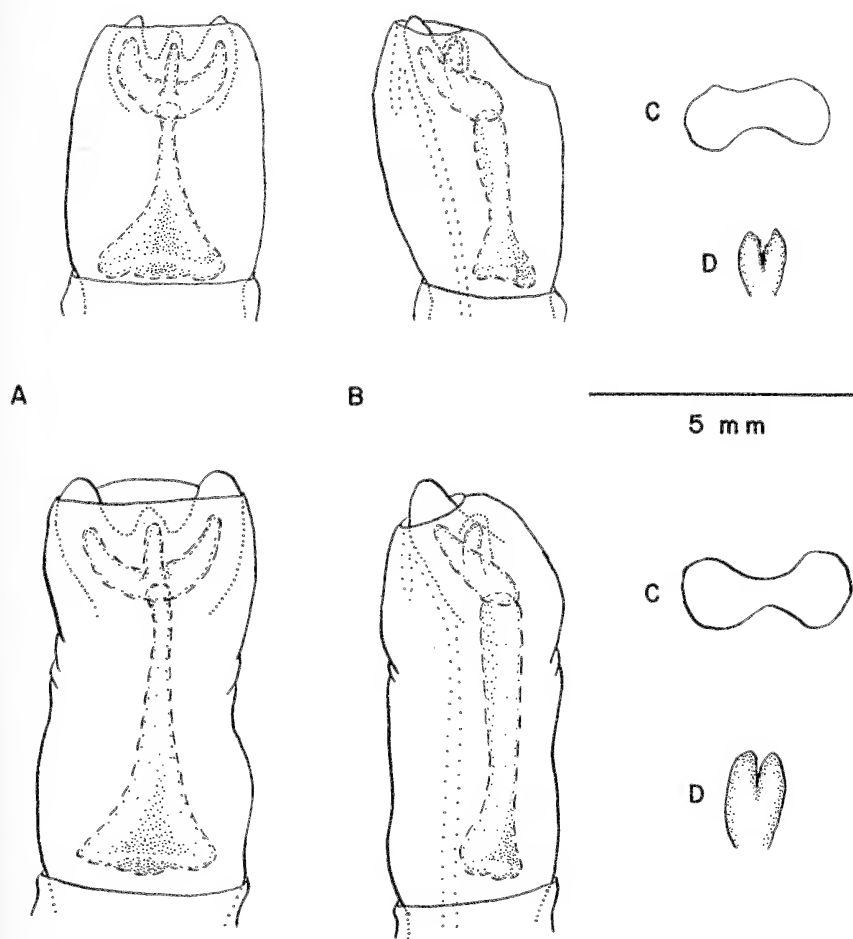


Fig. 5.—Phalli of *Andalgalomys*. Upper, *A. olrogii*; lower, *A. pearsoni*. A = ventral view; B = lateral view; C = outline of base of the baculum, its dorsal surface facing up; D = ventral view of urethral flaps. The drawings are composites.

broad; hairs on ventral body surfaces and upper surfaces of the feet white to their bases; pelage moderately long (hairs average about 10 mm on rump) and lax. Skull with wedge-shaped interorbital region; palatines with long slits in place of separate foramina; interparietal bones narrow, more or less wing-shaped in outline.

Etymology.—This species is respectfully and affectionately named in honor of Dr. Cläes Christian Olrog, who has made so many outstanding contributions to the knowledge of South America's fauna.

Table 1.—(Continued)

Andalgalomys obrogi																	Andalgalomys pearsoni																
Character	44020	44021	44022	44023	44024	M	SE	17562	17563	17566	17568*	17575*	17579	17580	M	SE	Calomys callosus M	Calomys muriculus M	Eligmodontia typus M	Graomys griseoflavus M													
No. palatine foramina, right	2	2	2	2	2	2	2	2	3	2	3	4	5	2	2.8	0.58	4	4	4	4													
No. palatine foramina left	2	2	2	2	2	2	2	2	4	3	3	2	4	3	3.2	0.37	4	5	4	4													
Incisive foramina intrusion	0.2	0.4	0.1	0.1	0.1	0.2	0.06	0.2	0.3	0.4	0.2	0.7	0.2	0.4	0.3	0.05	0.7	0.8	0.4	0.7													
M ¹ length	2.1	2.0	1.9	2.0	2.0	2.0	0.03	2.1	2.0	2.1	2.0	1.9	2.0	2.2	2.1	0.04	1.8	1.7	1.7	2.1													
M ² length	1.0	1.1	1.0	1.1	1.1	1.0	0.02	1.1	1.0	1.0	1.1	1.1	1.0	1.1	1.0	0.02	1.1	1.1	1.0	1.3													
M ³ length	0.9	0.9	0.9	0.8	0.9	0.9	0.02	0.8	0.9	0.9	1.1	0.8	0.8	0.9	0.9	0.02	0.8	0.9	0.6	1.1													
M ¹ width	1.4	1.3	1.3	1.3	1.3	1.3	0.02	1.3	1.5	1.5	1.4	1.2	1.5	1.5	1.5	0.04	1.2	1.1	1.0	1.5													
M ² width	1.1	1.2	1.1	1.2	1.2	1.2	0.02	1.0	1.2	1.2	1.2	1.1	1.2	1.4	1.2	0.06	1.1	1.0	0.9	1.3													
M ³ width	1.0	1.0	0.9	1.0	1.0	1.0	0.02	0.9	1.0	1.0	1.0	1.0	1.0	1.0	1.0	0.02	0.9	0.9	0.7	1.1													
Mandibular toothrow length	4.1	4.1	4.1	4.1	4.4	4.2 ^a	0.06	4.5	4.5	4.5	4.5	4.3	4.2	4.5	4.5	0.07	4.3	4.0	3.9	5.1													
M ₁ length	2.0	1.9	1.9	1.9	1.9	1.9 ^b	0.02	2.0	2.0	2.0	2.1	1.6	2.0	2.1	2.0	0.02	1.6	1.5	1.5	2.0													
M ₂ length	1.0	1.1	1.0	1.1	1.1	1.1	0.02	1.1	1.1	1.1	1.1	1.1	1.1	1.0	1.1	0.02	1.1	1.1	1.0	1.3													
M ₃ length	0.9	1.0	0.8	0.9	0.9	0.9	0.04	0.8	0.8	0.9	0.9	1.0	0.8	0.8	0.8	0.02	1.1	1.0	0.8	1.1													
M ₁ width	1.2	1.3	1.2	1.3	1.2	1.2 ^a	0.02	1.3	1.4	1.3	1.4	1.1	1.3	1.4	1.3	0.02	1.1	1.1	1.0	1.4													
M ₂ width	1.2	1.3	1.2	1.1	1.3	1.2	0.04	1.3	1.3	1.2	1.3	1.1	1.2	1.3	1.3	0.02	1.1	1.1	0.9	1.3													
M ₃ width	0.9	1.1	0.9	0.9	1.0	1.0	0.04	1.0	1.0	1.0	1.0	1.0	1.0	1.0	1.0	0.00	0.9	0.9	0.7	1.1													

* Immature, not used in statistical analyses.



Fig. 6.—Karyotype of *A. olrogi* male (CM 44022), from west bank Rio Amanao, about 15 km W (on Route 62) Andalgalá, Catamarca Province, Argentina.

Description.—External, cranial, and phallus measurements are presented in Tables 1 and 2. Characters are as described for the genus, elaborated below, and depicted in Figs. 1–5. Dorsal coloration is closest to Light Ochraceous Buff (capitalized terms from Ridgway, 1912), overlain with a light suffusion of black-tipped hairs, except on the sides, which are buffy, and on the face, which has a mixture of buffy and white hairs; regions around external nares, the dorsal-medial and posterior bases of the pinnae, and a spot below the pinnae are pure white; tops of feet and ventral parts, including the underside of the tail are white, the hairs being white to the base. Tail brownish above, moderately haired, slightly crested (hairs increasing in length on the dorsal surface toward the tip), and moderately pencilled (hairs extending about 5–9 mm beyond tip). Ears large, broad, and sparsely haired with fine, brownish hairs. Soles of feet naked, with six moderately large plantar tubercles (Fig. 4); plantar surfaces finely scutellate, and unpigmented (not blackish); first hind digit very short, not reaching the base of digits 2 to 4; tarsal elements of digits 2 to 4 somewhat elongated.

Table 2.—*Baculum and glans penis measurements of Andalgalomys.*

Species	Catalog no.	Glans		Baculum lengths			
		Length	Diameter	Total	Proximal bone	Medial digit	Lateral digit
<i>A. olrogi</i>	44020* CM	3.5	2.2	3.5	2.5	1.1	1.1
<i>A. olrogi</i>	44022 CM	—	—	4.4	3.0	1.2	1.4
<i>A. olrogi</i>	44023 CM	—	—	4.3	3.0	1.4	1.5
<i>A. pearsoni</i>	17568* UCONN	6.3	2.8	5.5	4.4	1.1	1.8
<i>A. pearsoni</i>	17575* UCONN	6.2	3.0	5.5	4.1	1.3	1.6
<i>A. pearsoni</i>	17580 UCONN	7.4	3.1	6.3	5.0	1.3	1.7

* Immature, baculum not fully ossified.



Fig. 7.—Creosote bush (*Larrea cuneifolia*) flat with associated mixed shrubs (*Acacia* and *Bulnesia*) and saguaro-like cacti (*Trichocereus*) in the background, west of Andalgalá, Catamarca Province, Argentina.

Bullae large; interparietal broad and narrow (in anterior-posterior aspect) in appearance (Figs. 1 and 2). Anteromedian style on anterior surface of M^1 well developed; mesostyle tiny, but apparent; anteroconule small, but evident; anterolabial style present and well developed, but not apparent in worn teeth (Fig. 3).

Phallus short and stubby; baculum about the same length as glans penis length (Table 2); baculum relatively robust; glans hood angled back sharply, being longer on the ventral surface than the dorsal surface (Fig. 5).

The karyotype is presented in Fig. 6. The diploid number is 60, and the number of autosomal arms is 116 (total arms number = 120); the X-chromosome is a large submetacentric and the Y-chromosome is a small submetacentric.

Comparisons.—*A. olrogi* differs from *A. pearsoni* in being lighter colored (lighter yellowish-brown and with less of a blackish overwash); in having relatively larger, broader pinnae; in its longer, laxer pelage; and in having a more hirsute and pencilled tail of longer length. Cranially, its bullae are more inflated and of longer length, its zygomatic arches are more robust, and its interparietals are shorter. The well-developed anteromedian style, the presence of a mesostyle, and the occurrence of a small anteroconule on M^1 are dental features that differ from *A. pearsoni*. The phallus of *A. olrogi* is shorter and stubbier than

that of *A. pearsoni* (Table 2 and Fig. 5), and has a unique dorsally-sloping hood.

A. olrogi is distinguishable from *E. typus* externally by its lack of hairy cushions on the hind feet and its longer tail. For other remarks concerning ways that *Andalgalomys* and *Eligmodontia* differ, see the generic description. *Calomys callosus* can be distinguished by its more volelike external appearance (that is, its small appendages, especially its shorter ears and shorter, non-pencilled tail).

Habitat and associates.—All five specimens were trapped in or near *Larrea* (creosote brush) stands, on fine-textured soils on the floor of the Bolsón de Pipanaco (Fig. 7). Trapping by Mares periodically over a six-year period in the same area, as well as south in Mendoza Province and northward through the provinces of Tucumán and Salta, has failed to produce any other specimens. *G. griseoflavus* is fairly common in the same area, but is generally captured only in *Prosopis* and *Acacia* trees along the arroyos or on rocky upper bajadas (Mares, 1976). *E. typus* and *C. musculus* were the only other cricetines trapped in the same habitat. *E. typus* is common on the creosote-flats. *C. musculus* is very rare in this habitat (being more common in riverine habitats, Mares, 1977c), and was captured only a single time in the same area as *A. olrogi*.

Remarks.—The holotype is somewhat immature and some skull characters are not fully developed (especially the supraorbital ledges). However, the dental cusps are largely unworn, and portray well the cusp patterns that are diagnostic for this species.

Specimens examined.—ARGENTINA. *Catamarca*: along Rio Amanao, about 13 km S, 15 km W Andalgalá, 1 ♂, skin, skull, phallus, and body in fluid (CM 44020); 10 km W Andalgalá (by road on Route 62, at km marker 10), 1 ♀, skin, skull, and chromosomes (CM 44021); West Bank Rio Amanao, about 15 km W (on Route 62) Andalgalá, holotype, plus 2 ♂, skins, skulls, phalli, and chromosomes (CM 44022, 44023).

Andalgalomys pearsoni (Myers)

Graomys pearsoni Myers, Occas. Pap. Mus. Zool., Univ. Michigan, 676:1, 18 March 1977.

Holotype.—Adult male; skin and skull, MVZ 145276; from 410 km NW Villa Hayes by road, Departamento Boquerón, Paraguay obtained 24 September 1973 by P. Myers, original No. 1161 PM.

Distribution.—Known from 0.5 km S Teniente Enciso, and 2.5 km S Teniente Enciso (km 655 Trans Chaco), Departamento Nueva Asunción, Paraguay; and from the type locality (Myers, 1977).

Diagnosis.—A moderately small, yellowish-brown mouse with a grayish overwash of black-tipped hairs; tail brownish, longer than head-body length, and sparsely haired (pencil <3 mm). Hairs on ventral surfaces and on feet white to their bases; pelage not noticeably

long or lax. Skull with wedge-shaped interorbital region; palatines with or without long slits; interparietals of short length and more or less wing-shaped in outline. Phallus relatively long, with moderately large and robust baculum.

Description.—External, cranial, and phallic measurements of five adult and two immature paratypes are presented in Tables 1 and 2. Characters are as described for the genus, elaborated below, and illustrated in Figs. 2, 3, and 5. Refer to Myers (1977) for additional illustrations and measurements. Color closest to Ochraceous-Tawny (Ridgway, 1912), overlain with a moderate to heavy suffusion of black-tipped hairs; tops of feet and ventral parts with hairs white to their bases; small white subauricular spot; face brownish, not noticeably lighter than dorsal parts of body (but without heavy suffusion of black); tail bicolored, brownish above and buffy-white below. Pelage of normal length (hairs on rump averaging about 7 mm). Tail of moderate length, sparsely haired, and with a very slight pencil (hairs <3 mm beyond tip). Ears of moderate size, not noticeably broadened, sparsely haired, and brownish in color. Soles of feet naked, with six medium-sized plantar tubercles; plantar surfaces coarsely scutellate, and darkly pigmented; first hind digit short; digits 2 to 4 not noticeably elongated relative to digit 5.

Bullae moderately inflated; interparietals of moderate length and somewhat wing-shaped. Anteromedian style on the anterior surface of M^1 obsolete (tiny or not visible); mesostyle absent; anterolabial style absent or rarely represented by a small shelf or style; anteroconule absent (Fig. 3).

Phallus relatively long, with the glans hood angled slightly ventrad (Fig. 5); baculum shorter than glans length, but relatively long and not noticeably delicate (Table 2).

Comparisons.—Refer to the account of *A. olrogi* for a comparison with that species. *A. pearsoni* is larger and with a much longer tail than sympatric *Calomys*. Its general appearance is not vole-like or *Mus*-like, differing in this respect from *Calomys*. For other characters that are useful in distinguishing *Calomys* from *A. pearsoni*, see the preceding generic description. From *G. griseoflavus chacoensis*, *A. pearsoni* can be distinguished by its smaller size, proportionately smaller ears, and its shorter, non-pencilled tail. For other details, refer to the generic description.

Habitat.—According to Myers (1977), *A. pearsoni* inhabits dry grasslands, which occur as islands in the western Chaco of Paraguay.

Specimens examined.—PARAGUAY. Nueva Asunción: Teniente Enciso, 4 ♂, 1 ♀, skins, skulls, and 2 phalli (UCONN 17562, 17563, 17566, 17568, 17575); 0.5 km S Teniente Enciso, 1 ♂, 1 ♀, skins, skulls, and phallus (UCONN 17579, 17580).

RESULTS AND DISCUSSION

Measurements for 38 morphometric traits for both species of *Andalgalomys*, and for comparable samples of other related phyllotines, are given in Table 1. Ten of the 38 characters are significantly different ($P \leq 0.05$) in *A. olrogi* and *A. pearsoni*. Five of these differences are highly significant ($P \leq 0.01$), despite the small sample sizes. Particularly distinctive measurements include tail length, bullar length, and interparietal length, all of which will readily distinguish *A. olrogi* from *A. pearsoni*.

Table 3.—Matrix of similarity for 51 dental characters. See the generic and species descriptions for the characters utilized. The values for species pairs indicate the number of shared characters between taxa. Unique traits indicates the number of traits not shared with other taxa.

Species	<i>Andalgalomys pearsoni</i>	<i>Calomys callosus</i>	<i>Eligmodontia typus</i>	<i>Graomys griseoflavus</i>	Unique traits
<i>Andalgalomys olrogi</i>	43	28	27	27	3
<i>Andalgalomys pearsoni</i>	—	39	29	29	0
<i>Calomys callosus</i>	—	—	40	34	0
<i>Eligmodontia typus</i>	—	—	—	31	3
<i>Graomys griseoflavus</i>	—	—	—	—	6

Bacular and glans penis data are listed in Table 2, and Fig. 5 illustrates the phalli of *Andalgalomys*. Unfortunately, we had no intact phalli from mature individuals of *A. olrogi* (but there are mature bacula); and two of the three phalli of *A. pearsoni* are immature with only partially ossified bacula. The mature bacula of *A. olrogi* are much shorter than *A. pearsoni*, but the two species are similar in relative size of the digits, in the general outline of the baculum, in the dorsal-ventral concavity of the basal bacular shafts, and in the ball-shaped distal end of the baculum. These similarities, especially the digit proportions (a smaller, more slender medial digit) and the dorsal inflection of the medial digit are a combination of characters unlike any illustrated by Hooper (1962) or Hooper and Musser (1964). The bacular shaft (osseous baculum) is similar to *Phyllotis osilae* and *P. magister* (Pearson, 1958), and *P. andinum*, *P. amicus*, and *P. (Auliscomys) pictus* (HersHKovitz, 1962). We know nothing of the cartilaginous digits in these taxa, however.

The shape of the glans penes of the *Andalgalomys* species appear to be divergent. How much of this is due to immaturity, how much is due to different preservation techniques of the glans available to us for study, and how much reflects real differences cannot be answered with certainty. *A. olrogi* is unique in its dorsally-canted hood. Otherwise, its glans penis resembles *C. callosus* (Hooper and Musser, 1964). The glans penis of *A. pearsoni* is not particularly similar to any of the phyllotines known to us, but is, perhaps, closer overall of *E. typus* than to others illustrated in Hooper and Musser (1964).

A numerical summary of the similarities in dental traits between *Andalgalomys*, *Calomys*, *Eligmodontia*, and *Graomys* is given in Table

3. These traits were evaluated qualitatively (for example, the presence or absence of a style, the shape of a tooth, the relative size of cusps, and the positions of folds). In tabulating similarities, subjective judgments were sometimes necessary, but we do feel that the numbers reflect the relative degree of similarity of the various genera to *Andalgalomys*. Note that *A. olrogi* and *A. pearsoni* share more traits (43) than either does with other genera, and that *A. pearsoni* is more similar to *Calomys* and to *Eligmodontia* (although all of the shared characters are not the same) than is *A. olrogi*. *A. pearsoni* is more variable than is *A. olrogi* (species with variable conditions for a trait were regarded as being similar to both those that possessed and those that lacked a trait). This is why *A. pearsoni* can share 39 traits with *Calomys*, whereas *A. olrogi* shares only 28. *Andalgalomys* is somewhat less similar to *Eligmodontia*, which has a different dental pattern. *Eligmodontia* has a somewhat hypsodont and relatively well-crested molar arcade. This could indicate some importance of insects in its diet, especially hard, chitinous species such as coleopterans. *Andalgalomys* is least similar to *Graomys*. *Graomys* has a relatively well-developed triangulate, planed, and hypsodont pattern that is familiar to many grazing and browsing species, including many of the more evolved phyllotines. *Andalgalomys* seems to be progressing towards a laminated and perhaps planed molar pattern.

Overall, we regard *Calomys* as the most primitive group of phyllotine species, and the ones closest phenetically to the oryzomyines. Primitive traits include their persistently brachydont, tuberculate dentition, their more classically "murine" skull (that is, a sharply ridged supraorbital region, relatively unconstricted interorbital region, and a robust rostrum), and their generally unspecialized appendages. The most divergent *Calomys* are somewhat akodonlike externally with the volelike suite of adaptations that most obviously includes shortened appendages and microtineline pelage. Populations of *C. callosus* from Catamarca, Argentina, illustrate this condition well. However, these tendencies are not nearly as well developed in *Calomys* as they are in some other phyllotines (and in akodonts and sigmodonts in general). We do think that some *Oryzomys* (especially *Oligoryzomys*) are not too unlike *Calomys*, although their dental differences are certainly trenchant.

In its non-dental morphological features, *A. pearsoni* is more primitive and closer to *Calomys* than is *A. olrogi*. Its somewhat harsher pelage, smaller and narrower ears, shorter and less-specialized feet, shorter and less-pencilled tail, less-inflated bullae, and greater number of palatine foramina are notably primitive characters for *Andalgalomys*. Overall, though, the similarities between *A. pearsoni* and *A. olrogi* are much greater than their differences. This is especially well

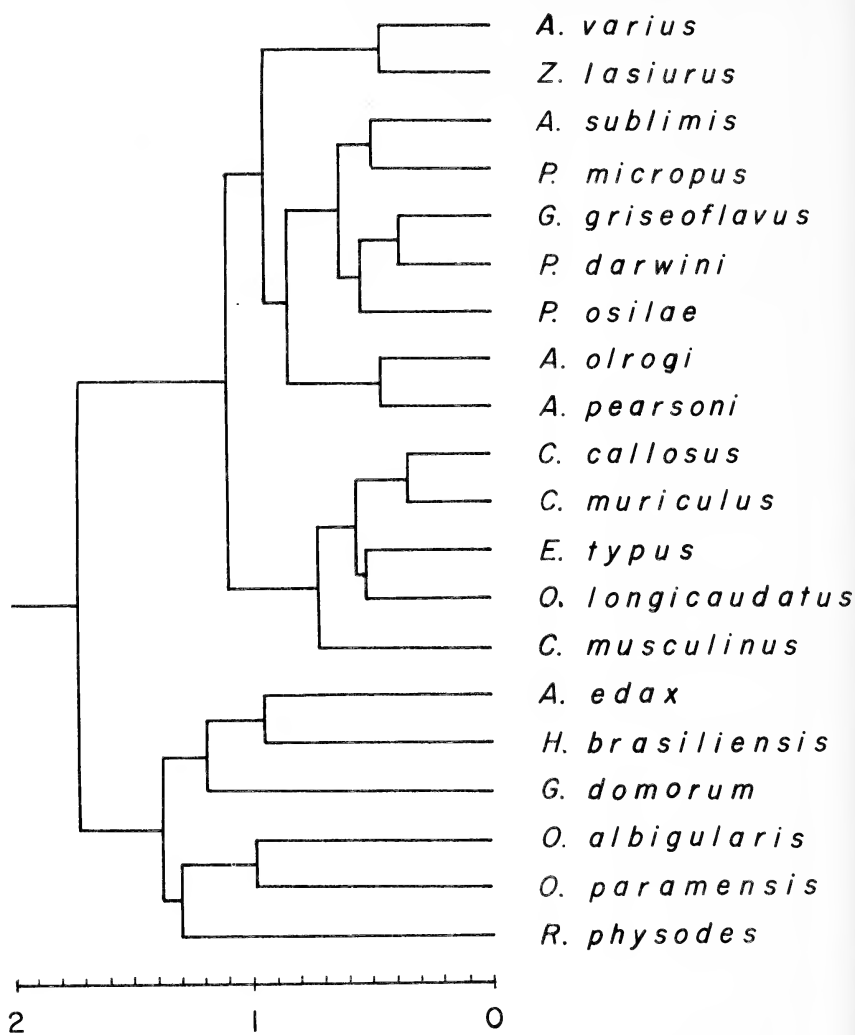


Fig. 8.—Phenogram, based upon taxonomic distance, of several South American cricetine species. The cophenetic correlation coefficient is 0.73.

illustrated by the results of the multivariate analyses of the morphometric traits.

The results of the numerical analysis based upon average Euclidean distance are shown in Fig. 8. Taxa with the lowest distance values are closest together in 38 dimensional space. The holotypes of *G. edithae* and *G. hypogaeus* were not included because we had no measurements

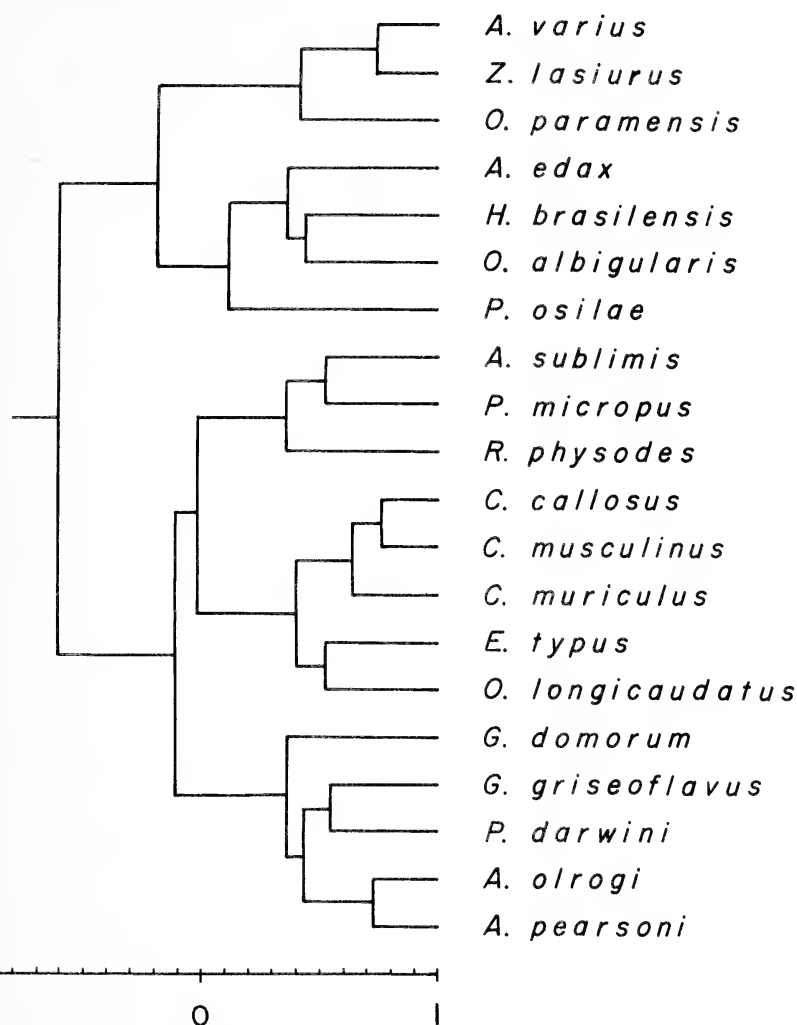


Fig. 9.—Phenogram, based upon Q-mode correlation coefficients, of several South American cricetine species. The cophenetic correlation coefficient is 0.78.

for several characters for these individuals. Note that *A. olrogi* and *A. pearsoni* are most similar to each other (distance = 0.47), and that *Andalgalomys* is most closely linked with a cluster that includes *Auliscomys*, *Phyllotis*, and *Graomys* (Fig. 8). *Akodon* and *Zygodontomys* are united with the above taxa, but are about equally similar phenetically (average taxonomic distance) to the cluster that includes *Calo-*

mys, *Eligmodontia*, and *Oryzomys longicaudatus*. Several relatively specialized, and generally dissimilar taxa, including *Andinomys*, *Holochilus*, *Oxymycteris*, *Oryzomys albigularis*, and *Reithrodon* are linked with a large *Graomys* (*G. domorum lockwoodi*).

A summary of the numerical analysis using Q-mode correlation coefficients is presented in Fig. 9. Taxa that are most similar in proportions will exhibit the highest positive similarity coefficients. *A. olrogi* and *A. pearsoni* are more similar ($r = 0.73$) to each other than are any other pair of taxa except for *Akodon* and *Zygodontomys* ($r = 0.74$). *Andalgalomys* is most similar, proportionately, to *P. darwini* and *G. griseoflavus* (Fig. 9). These taxa, in turn, are clustered with a group that includes *Calomys*, *Eligmodontia*, *O. longicaudatus*, *Auliscomys*, *P. micropus*, and *Reithrodon*.

The distance and similarity phenograms both show a strong phenetic relationship between *A. olrogi* and *A. pearsoni*. *Eligmodontia* is linked most closely with *O. longicaudatus* in both analyses, but is most similar phenetically to *Calomys*, among the phyllotines. Neither phenogram (Figs. 8 and 9) portrays precisely the relationships that we perceive subjectively from our examination of dental cusp patterns (Table 3) and of the karyotypic variation of phyllotines (Fig. 10). The phenograms are fairly accurate summaries of the morphological similarities (excluding dental cusp-patterns) of these taxa, although all of the intertaxa relationships cannot be shown in the phenograms. The co-phenetic correlation coefficients are not particularly high (0.78 for the similarity phenogram and 0.73 for the distance phenogram), indicating that considerable information is lost in the summaries. Furthermore, it should be stressed that the numerical methods utilized are measures of phenetic similarities. They do not distinguish between similarities due to parallelism, convergence, and common ancestry.

A discriminant analysis, utilizing measurements of *G. hypogaeus* (Cabrera, 1934) and *G. edithae* (Thomas, 1919) was performed in order to provide a quantitative assessment of their phenetic similarities to other taxa, and in order to attempt to classify them with one or more of these taxa. The characters used were the 13 measurements common to the two reports. The potential groups into which these forms could be classified by the analysis included *A. olrogi*, *A. pearsoni*, *C. callosus*, *E. typus*, and *G. griseoflavus*. Both *G. edithae* and *G. hypogaeus* were closest to *E. typus* in this analysis, with D^2 values of 45.3 and 92.9, respectively (the mean intragroup D^2 for *E. typus* was 11.3). These data should be interpreted with caution, as the characters utilized are not very diagnostic, and external dimensions and size have a heavy influence in these statistics. Our examination of the *G. edithae* holotype revealed several characters that are clearly not associated with *Eligmodontia*, but are representative of *Graomys*. Most notable

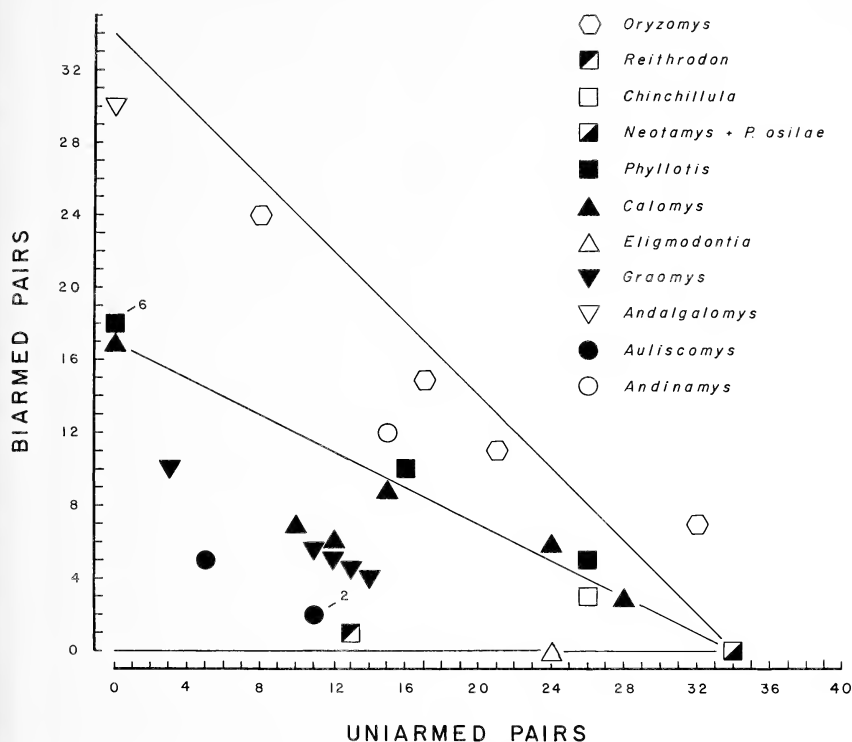


Fig. 10.—Autosomal karyotypic variation of phyllotine rodents and of *Oryzomys albigularis*. Arm additions (pericentric inversions or other addition processes) that result in changes in FN cause displacement along a line whose angle is depicted in the uppermost line. Robertsonian processes (changes in $2n$) result in numerical changes along the angle shown in the middle line. Tandem fusions (changes in $2n$ and FN) cause displacement to the left along a horizontal line such as the bottom line. The numbers indicate the number of species sharing the same karyotype, whereas unnumbered symbols indicate the karyotypes of single species. The data are from Pearson and Patton (1976), Gardner and Patton (1976), and unpublished data.

in this regard are the narrow procingulum of M^1 in *G. edithae*, which is deeply divided from the protocone-metacone by deep anterior median and lingual folds, and the deep major fold on the M^3 of *G. edithae*. The paratypes of *G. edithae* (from near Chumbicha, Catamarca, at an elevation nearly 2,000 m lower than the type locality), represent, in our opinion, *G. griseoflavus medius*. The skull of *G. hypogaeus*, as we know it from a cursory examination and from photographs, is clearly an *E. typus*. However, one of us (Williams) considers it probable that the skin of *G. hypogaeus* is not *E. typus*. This is so, because Cabrera

(1934) explicitly compares *G. hypogaeus* to *E. typus* and remarks upon the naked soles of *G. hypogaeus*, and because the tail is proportionately longer (142% of head-body length) than is typical of *E. typus*. Also, the tail has a well-developed pencil (about 10 mm in length) and the ear pinnae are larger than those of *E. typus* from the same general region. Whether or not the *G. hypogaeus* holotype is a composite of an *E. typus* skull and the skin of some other species cannot be resolved until the specimen can be carefully examined.

Karyotypically, *A. olrogi* is the most divergent of the phyllotines so far examined (Figs. 6 and 10). Its relatively high diploid number and all-biarmed complement makes it unusual among the Sigmodontini (see Gardner and Patton, 1976). The only species similar to *A. olrogi* is *Oryzomys albigularis* from Colombia. Comparison of the karyotype of *A. olrogi* with the figure of *O. albigularis* from Gardner and Patton (1976) suggests a striking similarity. Three centric fusions and the pericentric inversion of two acrocentric pairs of autosomes would convert the *Oryzomys* karyotype into a near copy of *A. olrogi*. However, we can see no grounds for such a supposition, as *Andalgalomys* is clearly a phyllotine. Its karyotype can be most easily derived from the karyotype of *Calomys sorellus* by a process involving only pericentric inversions (see Fig. 10) or other arm-addition processes. In the absence of contrary data, we prefer this simple explanation of the karyotypic relationships of *Andalgalomys*, particularly because it coincides with our interpretations of morphological relationships. The variation in the known phyllotine karyotypes (Pearson and Patton, 1976) is certainly not much greater than the differences within some genera (for example, *Perognathus*, Patton, 1970; Williams, 1978). Thus, at this point we do not attach any particular importance to the dissimilarity of *A. olrogi* to other phyllotine karyotypes, and doubt that data on comparative gross morphology of the chromosomes of phyllotines are particularly useful for generic groupings when considered alone.

In summary, most of the analyses point to a relatively close relationship between *Calomys*, *Eligmodontia*, and *Andalgalomys*. Dental traits, morphometric analyses, phallic morphology, and karyology are consistent in showing these affinities. We propose that a fairly generalized, dry-grassland or Chaco-dwelling, *Mus*-like Sigmodontini (that is, something like *Calomys*) was the prototype for the phyllotine group. *Andalgalomys pearsoni* has most of the characters that an annectant form between a *Calomys*-like ancestor and the more specialized phyllotines would be expected to exhibit. There is much evidence to support a close relationship between *Calomys* and *Eligmodontia*, although we regard the foot, tooth, and bullar specializations of *Eligmodontia* as sufficiently divergent to warrant generic separation. We see no convincing reasons however, to suggest a *Phyllotis* origin for *Eligmodontia*.

tia, as Pearson and Patton (1976) and Gardner and Patton (1976) have done.

The Gran Chaco, or thorn forest, of South America is an extensive, largely uninterrupted habitat, occurring from Brazil through central Argentina. During mesic periods of the Pleistocene, the Chaco was probably even more extensive than today, and intruded into areas that currently support xeric Monte Desert vegetation (the flora of which was largely derived from Chaco ancestors, Morello, 1958). We suggest that during earlier periods of the Pleistocene a form ancestral to *A. olrogi*, and probably similar in morphology to the generalized genus *Calomys*, was a widespread Chacoan species. As Chaco vegetation moved into the valleys of the Monte, this ancestral form was able to invade these areas. When the Chaco vegetation largely withdrew from areas such as the Bolsón de Pipanaco, a relictual population became progressively more adapted to xeric lowland conditions. Its habitat today is fine alluvial soil, supporting *Larrea cuneifolia* and interdigitations of gallery forests (*Cercidium*, *Prosopis*, *Acacia*, *Bulnesia*, and *Opuntia*; see Mares, 1975, 1977b; Orians and Solbrig, 1977; Fig. 7).

A. olrogi is relatively specialized for this desert habitat, exhibiting features common to desert-dwelling murids such as its lengthened and pencilled tail, lax pelage, inflated bullae and enlarged auditory pinnae, lengthened hind limbs, and reduced size of the lateral digits. In these features, *A. olrogi* exhibits remarkable convergence with gerbillines such as *Gerbillurus*. The convergence even extends to the development of palatal slits in *A. olrogi* (the slits are individually variable and less well developed in *A. pearsoni*), a feature common to gerbillines, but unknown in New World cricetines.

A. pearsoni is very likely more similar to the ancestral form and possesses more primitive traits than *A. olrogi*. It appears to be a non-forest offshoot of the hypothetical Chaco type, and today is apparently limited to islands of grassland within the Chacoan thorn forest (Myers, 1977). In such a habitat (which may be a persistent subunit of the generalized Chaco habitat) it can probably exist without serious competition from the larger, more arboreal *G. griseoflavus*. We visualize *Graomys* as specializing for exploitation of the thorn scrub and xeric monte habitats, and limiting *A. pearsoni* to intersylvan refugia.

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Massoia provided photographs of the skull of *G. hypogaeus*, and allowed Mares to examine the holotype. Finally, Mares thanks the many people of Andalgalá, who made his research enjoyable.

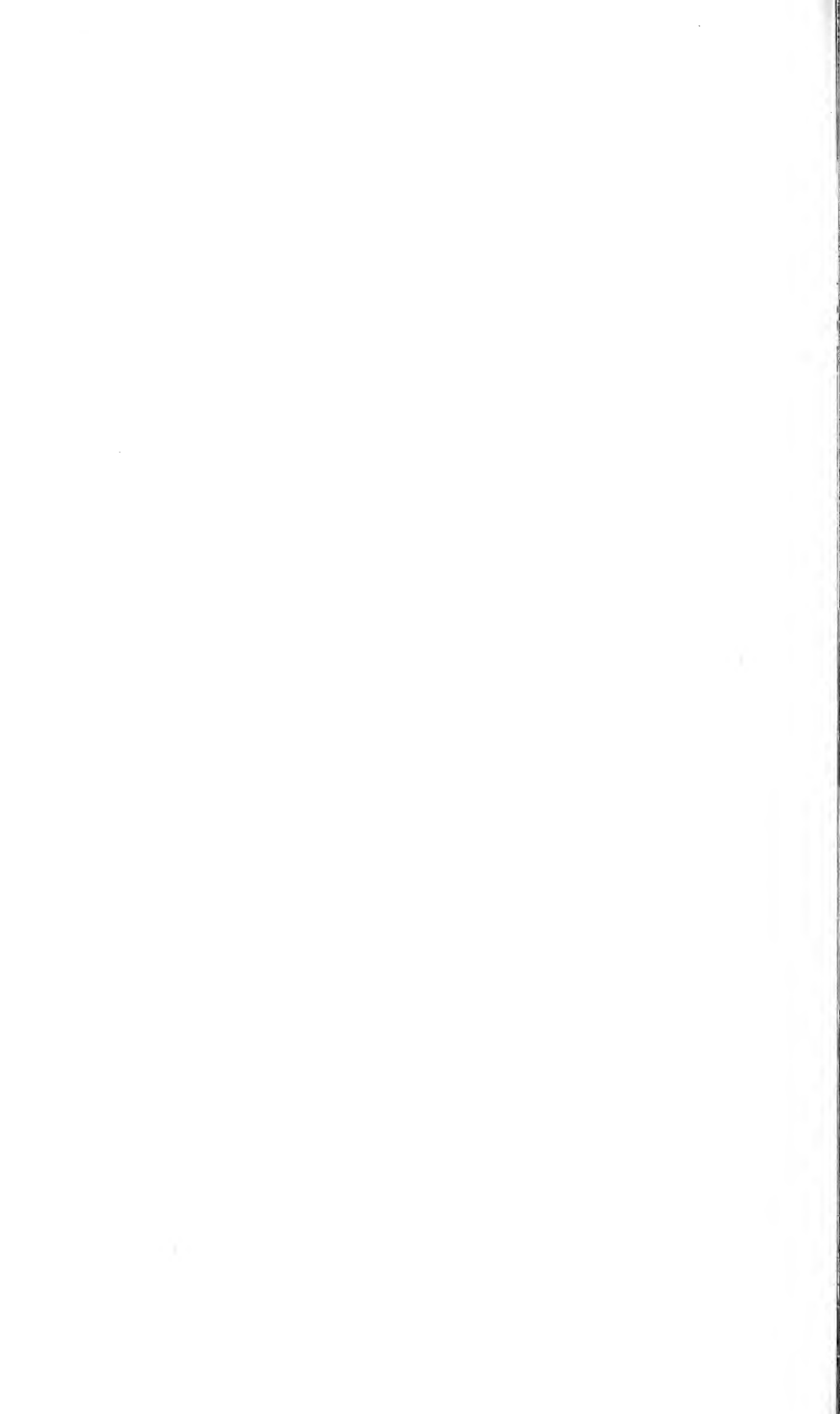
Travel to Argentina by Williams was funded by a Faculty Summer Grant from the Stanislaus State College Foundation. The Miguel Lillo Instituto Superior de Ecología of the Universidad Nacional de Tucumán kindly loaned Williams a vehicle for field use. California State College, Stanislaus, furnished field equipment. Rubén Barquez, Jorge Cajal, Tye Hafner, Ricardo Ojeda, and Connie Stuart assisted Williams in the field. Suzanne Braun provided much technical assistance during the course of this study. We are grateful for this, her drawing of Fig. 5, and for her editorial help. Drs. Sydney Anderson, Philip Myers, and Ralph Wetzel generously made specimens available for our studies. The expert rendering of Figs. 1 and 4 by Patricia Capllonch Barquez is greatly appreciated. Drs. Hugh Genoways, Philip Myers, and Oliver Pearson critically reviewed the manuscript.

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PALEONTOLOGY AND GEOLOGY OF THE BADWATER CREEK AREA, CENTRAL WYOMING PART 14. THE ARTIODACTYLS

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ABSTRACT

All artiodactyl material from the late Eocene faunas occurring along Badwater Creek in the northeastern part of the Wind River Basin, Wyoming, is described. Two indeterminate dichobunids are present together with a third form, *Apriculus praeteritus*. One indeterminate leptchoerid, two agriochoerids, *Diplobunops* and *Protoreodon*, the oromerycid *Malaquiferus*, four protoceratids, *Leptotragulus*, *Leptoreodon* and two species of *Poabromylus*, and a new genus of leptomerycid, *Hendryomeryx*, are described. Correlation is made with faunas in Texas, Utah, and California and the paleoenvironmental conditions are discussed. Relationships of the late Eocene selenodont artiodactyls are reviewed.

INTRODUCTION

Knowledge of late Eocene artiodactyls has been enhanced greatly in recent years through the work of Wilson (1971, 1974) and Golz (1976). Prior to these reports, Gazin's paper (1955) stood as the only major recent summary and his review of the dichobunids in that paper is still the only comprehensive study of that group for the late Eocene. As a result of their studies, the presence of the Hypertragulidae, Agriocheoridae, and Protoceratidae has been extended back into the late Eocene. Camelids are also present at that time but are only poorly represented and understood. The transition from basically low crowned bunodont forms to the higher crowned varieties of selenodont artiodactyls is a late Eocene event. By the beginning of the Oligocene

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Table 1.—*Artiodactyls in the Badwater faunas.*

Locality	Taxa
	Family Dichobunidae
5, 7	Dichobunids indet. (2 genera)
7	<i>Apriculus praeteritus</i>
	Family Leptochoeridae
Wood	Leptochoerid indet.
	Family Agriochoeridae
5, 6	<i>Protoreodon</i> cf. <i>P. petersoni</i>
5, 6, 20 and Wood	<i>Diplobunops matthewi</i>
	Family Oromerycidae
5, 6, 7	<i>Malaquiferus tourteloti</i>
	Family Protoceratidae
5, 6, 20 and Dry Fork	<i>Leptotragulus medius</i>
5, 6, 7	<i>Leptoreodon</i> sp.
20	<i>Poabromylus golzi</i> new species
7	<i>Poabromylus</i> cf. <i>P. golzi</i>
	Family Leptomerycidae
20	<i>Hendryomeryx wilsoni</i> new genus and species
Wood and Rodent	<i>Hendryomeryx</i> cf. <i>H. wilsoni</i>

the only bunodont forms, which are present, are the leptochoerids together with entelodonts and the newly evolved bunodont tayassuids.

Although the selenodont groups are present and radiating by the end of the Eocene, we still know little more about their origins than was known at the time of Gazin's (1955) review. In order to document the transition Dichobunidae to Agriochoeridae, Protoceratidae, Oromerycidae, Camelidae, and Hypertragulidae, we must know a great deal more about Bridgerian dichobunids, particularly forms from environments different from those at present represented in our collections (Black, 1968).

Artiodactyls are quite diverse in the Badwater fauna with thirteen species representing ten or eleven different genera and six families (Table 1). However, only the agriochoerids, the oromerycids, and one of the protoceratids are at all abundant. Gazin (1956) in the original work on the Badwater assemblage recorded seven genera, four of them known from only a single specimen. He also recognized three species of *Protoreodon* and one of *Diplobunops*. Although the new material described below consists for the most part of isolated teeth, there are a number of jaws and maxillae of many of the species and additional skull material of *Diplobunops*. There are, however, no unquestionable associations of upper and lower dentitions except for *Diplobunops*.

Artiodactyls are most abundant at localities 5 and 6, but this is probably more a sampling bias than a true reflection of occurrence. Quarries were opened at these localities in 1966 and 1967, whereas specimens from locality 7 and the Wood locality were collected through surface prospecting and washing operations. Some quarrying was also carried out at locality 20 with two rather complete maxillae and several jaw fragments recovered.

The three most abundant and widespread species are *Diplobunops matthewi*, *Malaquiferus tourtelotii*, and *Leptotragulus medius*. *Leptotragulus medius* is also found at Dry Fork about 20 mi to the east of the Badwater localities. Dichobunids, the oromerycid, *Leptoreodon*, and *Protoreodon* cf. *P. petersoni* are found only at localities 5, 6, and 7, localities, which are considered to be somewhat older than locality 20 and the Wood and Rodent locality. Locality 20 has yielded the type material of the new leptomerycid, *Hendryomeryx*, and this genus is only known from locality 20 and the Wood and Rodent localities. A new protoceratid is also found at locality 20 with possibly one tooth of this form from locality 7.

In general there is a greater diversity of artiodactyls in the earlier levels and the more primitive bunodont species occur only in these levels. The partially selenodont oromerycid, *Malaquiferus tourteloti*, is confined to the earlier faunal horizon. Only selenodont forms are represented in the upper faunal level with a concomitant drop in artiodactyl diversity in these levels.

All measurements are given in millimeters. Abbreviations are as follows: CM, Carnegie Museum of Natural History; USNM, National Museum of Natural History; a-p, anteroposterior; tr, transverse; N, number; M, mean; OR, observed range; SD, standard deviation; CV, coefficient of variation; m.y., million years.

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RELATIONSHIPS OF LATE EOCENE SELENODONT ARTIODACTYLS

Relationships of the late Eocene and early Oligocene selenodont artiodactyls of North America are shown in Fig. 1. The ancestral suite of characters included separate metapodials, separate radius and ulna, selenodont but brachyodont dentition with an enlarged metaconule and transverse molars. Small protoconules and mesostyles on the upper molars, the metaconule in the hypocone position and paracone and metacone ribs are shared derived characters for this group. From this ancestral condition one group arose which initially squared up the upper molar dentition and had the lower first premolar and canine of equal size. This protocamelid gave rise to two groups—the Oromerycidae and the Camelidae. The latter evolved elongate limbs with fused

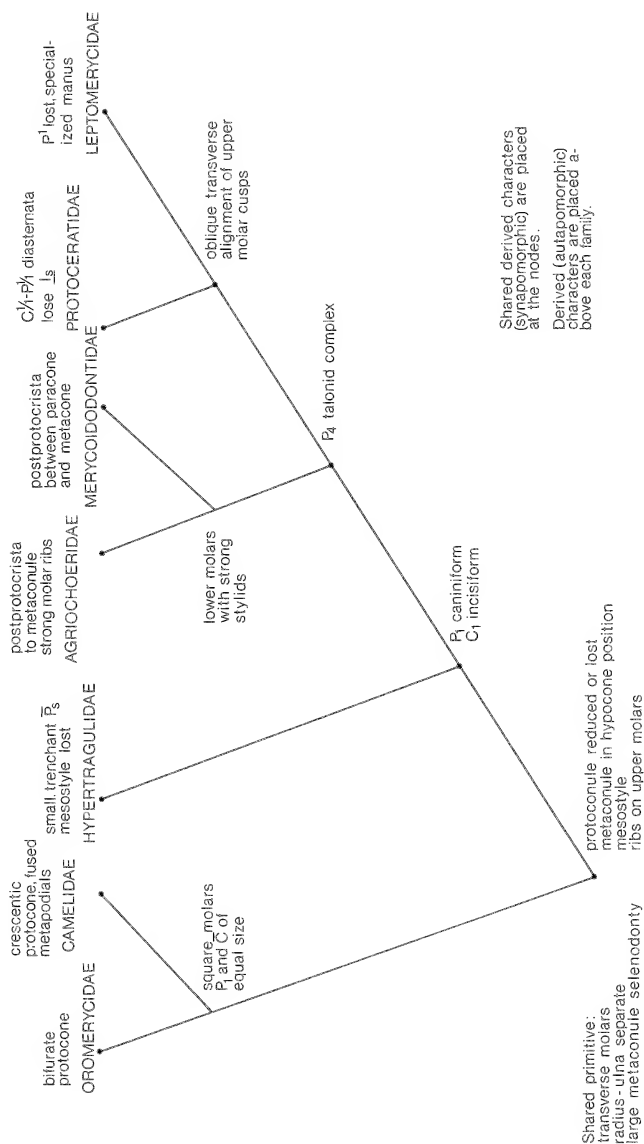


Fig. 1.—Diagrammatic representation of relationships of North American late Eocene selenodont artiodactyl groups.

metapodials and transversely compressed molars while the oromerycids maintained shorter, less reduced limbs and square upper molars. The protocone in the oromerycids became bifurcated while that in camelids became crescentic.

From the ancestral stock the remaining selenodont forms developed an incisiform lower canine and a caniniform P_1 . With loss of the upper incisors, the mesostyle and the evolution of small trenchant lower premolars the Hypertragulidae emerged. All other late Eocene selenodont groups developed a P_4 with a complex talonid and expanded the upper molars transversely. The Agriochoeridae and Merycoidodontidae evolved strong lower molar stylids with the agriochoerids emphasizing ribs on the upper molars and directing the posterior crest of the protocone towards the protoconule while the merycoidodonts developed only weak upper molar ribs or had none at all and directed the posterior crest of the protocone between the paracone and metacone.

The remaining selenodont groups known from the late Eocene evolved obliquely oriented upper molars with the protocone and metaconule positioned anterior to the paracone and metacone. One family, the Protoceratidae, evolved diastemata between the canines and P^1_1 and between P^1_1 and P^2_2 . This group also lost the upper incisors and fused the ulna and radius. The other family, the Leptomerycidae, evolved a specialized manus with reduction in carpals and lost P^1 . Of all the late Eocene selenodonts the leptomerycids appear to be the most highly specialized both in dentition and in limb structure.

I have refrained from arranging these late Eocene families in any classificatory scheme as a number of workers are reviewing particular families. However, I believe the relationships proposed in Fig. 1 to be reasonably valid.

PALEOENVIRONMENTS

The diversity and distribution of artiodactyl species at Badwater reflects not only a temporal sequence in the faunas but also a climatic change. Genera and species from localities 5, 6, and 7 occur earlier in time than do those at locality 20 and most probably the Wood and Rodent localities, and they also reflect a different environmental situation.

Selenodont species predominate throughout the Badwater sequence, but they are found together with a variety of bunodont forms in the lower faunal level, whereas no dichobunid species are known from the later localities and only one bunodont form, the earliest known leptchoerid, occurs in the upper level. Although three different dichobunids are present at Badwater, they are all represented by single individuals and are not as abundant as they are in the Uinta Basin. This suggests that early in the Badwater scenario there were areas,

Table 2.—*Diversity of late Eocene artiodactyls (based upon Utah, Gazin, 1955; California, Golz, 1976; Texas, Wilson, 1971, 1974; Wyoming, this paper). Bunodont genera and species are considered to be those in the families Dichobunidae and Leptochoeridae while the Agriochoeridae, Leptomerycidae, Protoceratidae, Oromerycidae, and Camelidae are considered to be selenodont groups.*

Age and region	Number of genera		Number of species	
	bunodont	selenodont	bunodont	selenodont
Early Chadronian				
Texas (Porvenir)	0	7	0	8
Duchesnean				
California (Pearson Ranch)	0	5	0	5
Utah (LaPoint)	0	3	0	4
Uinta C and Randlett				
California	1	4	1	10 ¹
Utah	4	6	4	14 ²
Texas	0	3	0	4 ³
Badwater 5, 6, 7	3	6	3	6
20 and Wood	1	5	1	5
Uinta B				
California	0	4	0	5
Utah	4	6	6	8 ⁴

¹ Four species of *Protylopus* and 4 species of *Leptoreodon*.

² Seven species of agriochoerids.

³ No oromerycids of dichobunids.

⁴ Six species of dichobunids.

probably along the stream banks, where the vegetation was dense and of a tropical nature, much as in the Uinta Basin but that this type of habitat was restricted. Dichobunid dentitions would seem to be adapted for browsing on plant material less abrasive than that eaten by artiodactyls with a selenodont type of dentition. The dichobunid dentition is one that functions more to crush and pulp than to cut and grind.

At Badwater there are a variety of selenodont species, at first with the dichobunids and later by themselves. Some of the later species, particularly *Leptotragulus medius*, *Hendryomeryx wilsoni*, and *Poabromylus golzi*, are probably the most advanced late Eocene selenodont artiodactyls yet known.

The occurrence of these species and the diversity of the selenodont forms indicates the presence of a diversity of more abrasive food resources, perhaps even the presence of more open savanna woodland in areas away from the stream borders and perhaps higher on the mountain slopes. Webb (1977) suggests that the appearance of selenodont artiodactyls heralds the appearance for the first time in North America of a more open savanna or savanna woodland environment.

He notes that paleobotanical evidence supports the thesis that savanna woodland was developed on the lower slopes of the Rocky Mountains by late Eocene time and that it was maintained there by the dry winter seasons. He also notes the presence of grasses as indicated by pollen as a part of this savanna complex. Webb suggests that the late Eocene and early Oligocene savanna woodland in the Rocky Mountains resembled that occurring today in the Chihuahuan regions of Mexico.

Perhaps the development of savanna woodland occurred first on the Rocky Mountain slopes in response to greater seasonal temperature fluctuations than were to be found in the coastal regions of California or to the south in Texas. There is certainly a greater diversity of selenodont artiodactyl types at Badwater than have been found either in California or Texas at a comparable time (Table 2).

It is toward the end of the Eocene that filling of the intermontaine basins had progressed to the point where only the higher cores of the mountain ranges were left above the surrounding plains surface. This topographic change was undoubtedly accompanied by a floristic change with a variety of new herbs, shrubs, and trees on the landscape, perhaps similar to what MacGinitie (1953:58–59) referred to for the early Oligocene of the central Colorado Rocky Mountains as "sub-humid grassy shrub probably similar to the thorn bush and the mesquite grass formation of southwest Texas with more mesic vegetation in wide flood plains." There was certainly a variety of hardier, more drought-resistant plants on the scene in the late Eocene than had been present earlier in the Eocene. The new vegetation provided new food resources for the artiodactyls and the first suggestion of these new artiodactyl assemblages is seen in the Badwater faunas.

Webb (1977) is of the opinion that most of these new selenodont artiodactyl types were immigrant from Asia in the late Eocene. He lists camelids, hypertragulids, leptomerycids, and agriochoerids as definite immigrants from Asia, with the oromerycids, protoceratids, and merycoidodontids as possible immigrants. It is true that we are unable to trace the origins of these families into middle Eocene artiodactyl groups. However, Radinsky (1965, 1969) has demonstrated that Asia, during the late Eocene, was the center of perissodactyl radiation for both tapiroids and rhinocerotoids, and that very few artiodactyls were present in the late Eocene faunas of Asia. Therefore, most of the late Eocene selenodont artiodactyls found in North America could well be of New World origin evolving higher on the Rocky Mountain slopes or perhaps at more northern latitudes.

FAUNAL CORRELATION

Because of the varieties of different habitats sampled in California, Utah, Texas, and Wyoming, precise correlation of the faunas from

these regions is difficult. The lack of radiometric dates for most of the faunas also exacerbates this problem. There are no radiometric dates known for most of the classic Eocene sequence in the Uinta Basin of Utah and only one date of 39.3 m.y. published for the contact of the Halfway and LaPoint members of the Duchesne River Formation (McDowell et al., 1973). No K-Ar dates have been published for the late Eocene sequence in California, whereas a series of three dates bracket the Candelaria fauna in West Texas. The earliest, 40.2 ± 2.9 m.y., comes from below the fauna, whereas a date of 38.6 ± 1.2 m.y. comes from the Buckshot Ignimbrite, which overlies the fauna (Wilson et al., 1968). One date of 41.2 ± 1.4 m.y. is known for the Badwater sequence (Black, 1969) associated with the fauna from locality 20.

All of the dates known at present are associated with faunas of latest Uintan or Duchesnean aspect with no potassium-argon dates available for the classic faunas from most of Uinta time. Recent, as yet unpublished, work in the northwestern corner of the Wind River Basin and in the Washakie Basin will change this picture considerably. One other earlier date from Badwater of 45.0 m.y. (Evernden et al., 1964) is not associated with an identifiable fauna.

Some correlations can be made based on the occurrence and stage of development of the various artiodactyl species. No dichobunids are known for any of the faunas after Uinta C time, with only selenodont species occurring at locality 20, and in the Candelaria, LaPoint, and Pearson Ranch faunas (Table 2). Earlier, during Uinta C time, dichobunids are common in Utah and occur, but are scarce, in California and at Badwater. The difference in abundance and diversity during this time is, as has already been discussed, a reflection of differing habitats in the three regions. Agriochoerids and leptotraguline protoceratids occur in all four regions with the greatest agriochoerid diversity found in the Uinta Basin. *Diplobunops* is restricted to the intermontaine region, whereas *Protoreodon* is found in all late Eocene faunas.

Oromerycids are diverse in the Uinta C assemblages in California with four or five species of *Protylopus* present. In the interior only one species of oromerycid, *Protylopus annectens*, is present in the Myton fauna and the distinctive genus *Malaquiferus* in the Badwater Uinta C fauna. No oromerycids are present in the later Badwater fauna or in Texas until Oligocene time.

The earliest leptomerycid, *Hendryomeryx*, is known only from the younger Badwater faunas and from the early Oligocene Porvenir fauna of Texas. Camelids are known in California and in Utah, although sparsely represented, but are not found at Badwater or in Texas. Finally, the more advanced protoceratid, *Poabromylus*, is known only

from the LaPoint fauna in Utah, from Badwater, and from the Candelaria and Porvenir faunas in Texas.

Badwater localities 5, 6, and 7 correlate best with the Myton fauna of Utah and the Tapo Ranch, Laguna Riviera faunas of California. The Badwater locality 20 fauna is younger than the above but older than the LaPoint and Candelaria faunas and somewhat older than the Pearson Ranch fauna. The advanced aspect of some of the artiodactyls found at locality 20 is most probably due to their occurrence in a dry, more open, and perhaps more upland, situation.

SYSTEMATIC REVIEW

Order ARTIODACTYLA Owen, 1848

Family DICHOBUNIDAE Gill, 1872

Dichobunids are uncommon in the Badwater faunas with probably only three species represented, one from locality 5 and two from locality 7. Dichobunids are not common elements of any of the late Eocene faunas, but they are much more diverse in the Uinta Basin sequence than anywhere else in North America during this interval.

In California only a single dichobunid is known, *Tapochoerus egressus* from Tapo Ranch. No dichobunids are known from the late Eocene of Montana, nor from the Texas late Eocene faunas, but *Pentacemylus* is known in both places in the early Oligocene. In the Uinta Basin at least 11 species representing seven genera of dichobunids are present during Uinta B and C time, but no dichobunids persist above the Randlett horizon. The number and diversity of dichobunids in the Washakie Basin late Eocene is difficult to determine; these faunas are under study by William Turnbull. No new material of *Apriculus praeteritus* has been recovered during our work at Badwater. The species is known only from the type specimen. The other dichobunids present are represented by single teeth and cannot be assigned to genus.

***Apriculus* Gazin, 1956**

Apriculus praeteritus

Holotype.—USNM 21100, RP⁴-M³.

Locality.—Probably locality 7.

Diagnosis.—Upper molars nearly quadrate with large lingually placed metaconule and simple conical cusps; no hypocone; no external styles; cingula continuous around molars; protoconule larger than in *Helohyus*.

Discussion.—Gazin (1956) provided an adequate description of the type and only known specimen. He suggested that *Apriculus* was descended from *Helohyus*. There are no known later descendants.



Figs. 2-4.—2) *Dichobunid* indet., CM 14552, RM², $\times 3.5$. 3) *Dichobunid* indet., CM 19785, LM³, $\times 3$. 4) *Leptochoerid* indet., CM 16097, LM₂, $\times 3.5$.

Dichobunids indet.

Figs. 2 and 3

Specimens.—CM 14552, RM² from locality 5 and CM 19785, LM³, from locality 7; USNM 20560, one half LM₃, locality not known.

Description.—The M² is broken along the buccal border so that part of the paracone, the mesostyle, and the metacone/metastylar region are missing. The tooth has a greater transverse than anteroposterior width. The protocone is large and joins a distinct protoconule through a narrow crest. The protoconule in turn sends a crest into the parastyle. A large hypocone is present, isolated from both the protocone and metaconule. The latter is large. A short anterior cingulum is present below the protocone.

The M³ is almost triangular in occlusal outline with the protocone situated at the interal apex. All cusps are rather high and sharp. There is a small parastyle and mesostyle but no metastyle. The protoconule and metaconule are large, sharp, and have both anterior and posterior crests. Those from the protoconule pass anteriorly to the parastyle and posteriorly to the base of the paracone; those from the metaconule are more isolated. The protocone and protoconule are connected about midway down the side of each cusp. Prominent anterior and posterior cingula are present, as is the stylar shelf. There is no hypocone.

Gazin (1956) referred a partial M₃ to *Pentacemylus*. The fragment is dichobunid but little more can be said about it.

Discussion.—The M² is somewhat reminiscent of that tooth in *Hylomeryx* and *Mytonomeryx* but one does not know whether a mesostyle was present, or not. The complete isolation of the hypocone clearly distinguishes the tooth as that of a dichobunid rather than a hyposodont condylarth.

The M³ is peculiar in possessing sharp cusps and a triangular shape. It resembles the M³ of *Pentacemylus* somewhat, but the internal margin is much more acute than in that genus. The tooth might be an M³ of *Auxontodon gazini* for which no upper dentition is known.

	Measurements	
	a-p	tr
CM 14552	6.25	—
CM 19785	5.86	8.20

Family LEPTOCHOERIDAE

Van Valen (1971) reduced the Leptochoeridae to a subfamily of the Dichobunidae saying only that, "They (Leptochoeridae and Dichobunidae) are sufficiently similar that familial separation seems unnecessary, so I reduce the Leptochoeridae to a subfamily (Leptochoerinae) of the Dichobunidae." I disagree and retain the family Leptochoeridae. The premolar dentition of *Stibarus*, *Leptochoerus*, and *Nanochoerus* is quite derived and differs markedly from that of any dichobunids. The pronounced reduction in the size of the molars from M^1_1 to M^3_3 also separates these families (Macdonald, 1955). Gazin (1955) suggested that the Leptochoeridae were possibly derived from *Diacodexis*, but he indicated that no intermediate forms were known between the Lost Cabinian *Diacodexis* and the first leptochoerid. The latter have not been previously reported from any Eocene fauna. The earliest known leptochoerids are the early Oligocene *Stibarus yoderensis* from the Yoder Formation of Wyoming and *Nanochoerus montanus* from Pipestone Springs, Montana (Macdonald, 1955). It is somewhat surprising that so little is known about the middle and late Eocene history of the family. West and Atkin (1970) have suggested that the Bridgeran *Neodiacodexis* may be related to the leptochoerids.

Stibarus is described as having paraconids on the lower molars, whereas *Nanochoerus* molars do not retain the paraconid. On this basis the single tooth described here is closer to *Stibarus* than to other Oligocene leptochoerids. It is smaller than any known Oligocene form. The single tooth from Badwater only serves to indicate that the family had differentiated by the late Eocene. Much more middle and late Eocene material will be needed to understand this origin.

Leptochoerid indet.

Fig. 4

Referred material.—CM 16079, LM₂.

Locality.—Wood locality.

Description.—The tooth is smaller than that of any other known leptochoerid, but it is morphologically almost indistinguishable from the M₂ of early Oligocene *Stibarus*. The trigonid is compressed anteroposteriorly with the paraconid still distinct as the tooth is unworn. With little wear the paraconid and metaconid would become one broad cusp. There is a distinct lophid from the protoconid to the metaconid. The trigonid basin is somewhat open posteriorly, more so than in the early Oligocene form. The protoconid and metaconid are of equal size with the hypoconid somewhat smaller and lower. There is a continuous anterior cingulum from the base of the parametaconid to the buccal face of the protoconid. The buccal valley is acute with the anterior crest from the hypoconid passing anterolingually into the protoconid-metaconid slope at the point where the trigonid basin opens posteriorly. A very small metastylid lies on the posterointernal face of the metaconid. The entoconid is broken away but was obviously separated from the metaconid by a deep notch. A small hypoconulid is present together with a narrow posterior cingulum.

Measurements

	a-p	tr
CM 16079	4.00	3.25

Discussion.—This single tooth appears to be unmistakably leptocherid in morphology. The paraconid is perhaps somewhat more distinct than in the Oligocene form and the principal cusps not as rounded and heavy. However, nothing can be said about leptocherid origins on the basis of a single tooth. It is of interest in indicating that the family had differentiated by the late Eocene.

Family AGRIOCHOERIDAE Leidy, 1869

In his paper on the Badwater fauna, Gazin (1956) recognized two large agriochoerids, *Protoreodon pearcei* and *Diplobunops* cf. *D. matthewi*, together with two small protoreodont species, *Protoreodon* cf. *P. petersoni* and *P. near P. pumilus*. In the larger collection now available, I have been unable to distinguish *P. pumilus* from the large agriochoerid present, which I consider to be *Diplobunops matthewi*.

Peterson (1919) originally described *Diplobunops matthewi* from Myton Pocket, Utah, based upon fragmentary skeletal, maxillary, and jaw material. He later described a second species *D. uintensis*, from northeast of Ouray, Utah (possibly what is now called Leota Bench), based upon a good skull. Gazin (1955) synonymized these two species and described a new form, *D. vanhouteni*, from the White River Pocket, Utah. A third species is also known, *D. crassus*, described by Scott (1945) from the Randlett Member of the Dushesne River Formation. This latter form, based on a nearly complete skull, is the largest known species of the genus.

In the Uinta Basin sequence *Diplobunops* is always the largest of the agriochoerids present in any level and only a single lineage appears to be present. From its inception *Diplobunops* is distinguished from *Protoreodon* by characters of the rostrum and anterior premolar dentition. In other dental and postcranial characters the two genera are essentially identical. Although Gazin (1955) spoke of the less selenodont and somewhat more transverse molars in *Diplobunops*, there is too much variation in these rather subjective characters for their use as diagnostic features.

In the largest of the late Eocene agriochoerids, there appears to be a great degree of what I interpret as sexual dimorphism. This is particularly evident in the Badwater sample, which consists of four good skulls, an additional snout, and many partial dentitions. In this sample, it is impossible to recognize more than one somewhat variable species based upon characters of the skull, jaw, and dentitions. However, there are two discrete morphologies for the snout, canines, and anterior premolars. Gazin recognized this state of affairs when he wrote

(1956:28–29), “The distinction between *Diplobunops* and *Protoreodon* on the basis of isolated teeth is difficult to make, particularly in the Badwater materials, because with the recognition of the equally large *Protoreodon pearcei* size is no longer an aid.”

Complete skulls in this sample do, however, display some differences. In USNM 20305, and CM 19726 and 19728 there is a diastema between the canine and P¹ and between P¹ and P². The snout in these skulls is elongate and broad and the canine large. This is very similar to the condition in a skull of *D. matthewi* from Uinta C, CM 11769. In the skull that Gazin made the type of *Protoreodon pearcei*, USNM 20305, the rostrum is slightly shorter (canine to posterior end of M³: 95 mm as opposed to 103 mm) than in CM 11769, the skull of *D. matthewi* and, while there is a canine to P¹ diastema, there is no P¹ to P² diastema (Gazin, 1956: Plate 3, Figs. 7–8). The canine in USNM 20305 is slightly smaller than in USNM 20303.

These rostral and dental differences in the Badwater sample are taken to reflect sexual dimorphism in a single population considered to represent *Diplobunops matthewi*. On all other skull and postcranial characters, the sample cannot be separated. Therefore, I am convinced that only one species of large agriochoerid is present in the Badwater fauna and that this form was conspecific with the Uinta Basin species. A smaller agriochoerid is also present in the Badwater fauna and is referred to *Protoreodon* cf. *P. petersoni*.

In California during the late Eocene, there is but a single species of *Protoreodon* present at any time (Golz, 1976:29, Fig. 7) beginning with *Protoreodon* cf. *P. parvus* in the Friars Formation, followed by *P. pumilus* in the Santiago and Sespe formations and finally by *P. pacificus* in the Pearson Ranch fauna of Duchesnean age. There is no large agriochoerid of *Diplobunops* size. This is in contrast to the diversity of *Protoreodon* species found in the intermontaine regions of Utah and Wyoming, and in Texas.

The greatest diversity of agriochoerid species is recorded from the late Eocene sequence in the Uinta Basin, Utah, where two species of *Diplobunops* and at least four and possibly five species of *Protoreodon* occur in the Uintan and Duchesnean intervals. In Texas two species of *Protoreodon* occur in the Candelaria fauna of Duchesnean age while one species of *Protoreodon* and one of *Agriochoerus* are present in the early Chadronian Porvenir fauna.

Diplobunops Peterson 1919

Diplobunops matthewi

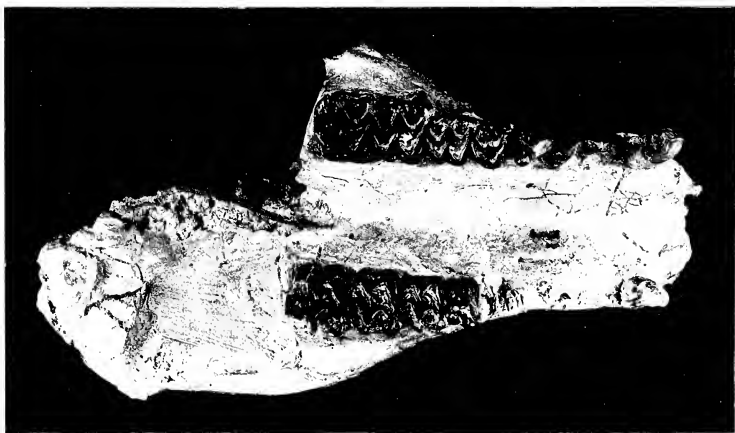
Figs. 5–11

Diplobunops matthewi Peterson 1919, pp. 62.

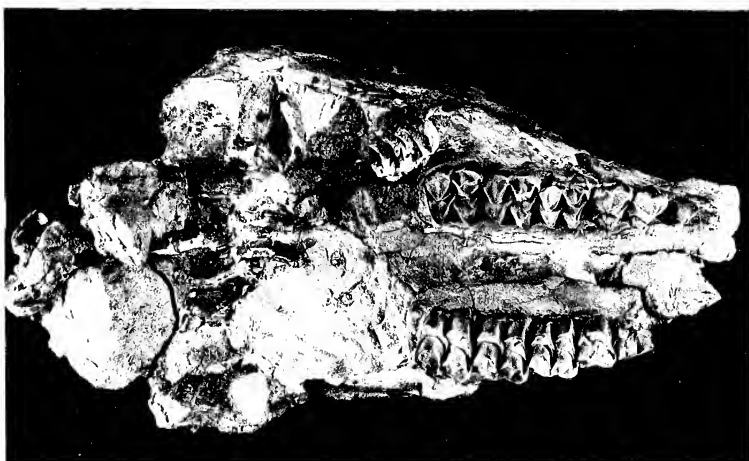
Protoreodon, near *P. pumilus* Gazin 1956, pp. 26.



5



6



7

Figs. 5-7.—*Diplobunops matthewi*, all $\times 1/2$. 5) Dorsal view of skull, USNM 20305. 6) Palatal view of same. 7) Palatal view of skull, CMNH 19728.

Protoreodon pearcei Gazin 1956, pp. 27.

Diplobunops cf. *matthewi* Gazin 1956, pp. 28.

Referred material.—USNM 20303 skulls and jaws, USNM, 20304, skull; CM 19728, skull; 17506, RP²-M³ and LP³-M³; 19726, R and LP²-P⁴; 14453, LdP³-dP⁴; 15751, LdP³-dP⁴-M¹; 19766, LM¹-M²; 17505, LM¹-M²; 17505, LM¹-M²; isolated upper teeth, 14450, 14477, 14537, 14544, 14590, 14595, 15387, 15333, 15752, 15755, 15931, 16059, 16777, 16780, 18252, 19556, 19730, 19733; 25334, RP₁-M₃; 19726, RP₁-P₄, M₂, LP₄-M₁; 19727, LP₃-M₃; 19729, R and LP₂-P₃; 14533, LP₂-P₃; 16055, RP₂-P₃; 19732, RP₃-dP₄; 15748, LP₃-dP₄-M₁; 14555, RdP₄-M₁; 16061, LdP₄-M₁; 14479, 29000, RP₄-M₁; 19765, RP₄-M₁; isolated lower teeth, 14434, 14435, 14439, 14467, 14551, 14552, 14586–14589, 14597, 15389, 15390, 15399, 15587, 15476, 15447, 15749, 15750, 15985, 16056, 16057, 16058, 16754, 16799, 17513, 17514, 17516, 21983, 21984, 21986.

Description.—Gazin (1955), Wilson (1971), and Golz (1976) have all given detailed descriptions of agriochoerid dentitions, which do not need to be repeated here for *Diplobunops matthewi*. The Badwater sample shows the P⁴ variation described by Wilson (1971:8–9) with some specimens having a partially divided parametacone while others show but a single cusp. On the molars the protoconule is generally present but becomes smaller from M¹ to M³. On one specimen (CM 17506), however, the protoconule appears to be absent on M³ and greatly reduced on M¹-M².

Sexual dimorphism is seen in the skull and jaws with some specimens displaying a short diastema between the upper canine and P¹ and between P¹ and P², whereas other specimens only have the canine-P¹ diastema. In the lower dentition some individuals have a P₁-P₂ diastema while in others there is no lower diastema at all.

In dental dimensions (Table 3) the Badwater sample of *Diplobunops matthewi* is no more variable than the Uinta Basin samples of *Protoreodon* measured by Wilson (1971: Tables 4–10). The coefficient of variation for most measurements lies between 4 and 9. All morphological and mensural data indicated that only a single, large agriochoerid is present in the Badwater fauna. Most of the specimens come from localities 5 and 6, with only three specimens known from locality 20 and two from the Wood locality.

Discussion.—Wilson (1971: Fig. 3) suggested that *Protoreodon pearcei* was ancestral to *Agriochoerus* and placed *Diplobunops* as a side lineage of Eocene agriochoerids without descendants. While synonymizing *P. pearcei* with *Diplobunops matthewi*, I still believe Wilson was most probably correct in deriving *Agriochoerus* from the large late Eocene agriochoerid complex. The reduction, and in some cases absence, of the protoconule on M¹-M³ in some of the Badwater specimens and the derived parametacone of P⁴ suggests this relationship.

Measurements of a-p length dentitions of *Diplobunops matthewi*
from Badwater

		C-M ³	P ¹ -M ³	P ¹ -P ⁴	M ¹ -M ³
USNM	20305	90.5	73.9	36.0	39.1
		95.6	—	—	40.0
CM	19728	—	—	—	41.1
		—	—	—	39.9
	19726	—	—	46.2	—
	17506	—	—	—	35.4
					35.4

		P ₁ -M ₃	P ₁ -P ₄	M ₁ -M ₃
USNM	20405	79.2	36.0	43.4
		82.0	38.0	43.5
CM	25334	88.8	43.3	45.6
	19726	—	43.2	—

Protoreodon Scott and Osborn, 1887

Protoreodon cf. *P. petersoni*

Referred material.—USNM 21101, RM¹-M³; CM 15977, LP²-dP³, 14525, 15413, 15414, 15754, 15757, 19731, isolated upper molars; 16055, RP₂-P₃.

Description.—There are only a few specimens of this small agriochoerid in the collections. As Gazin (1956:26) noted, the protoconule is weak on the upper molars. These specimens are all quite close to *P. petersoni* in size and are tentatively referred to that species.

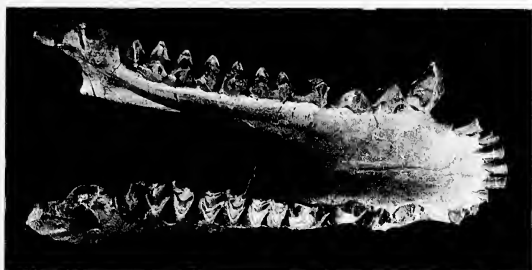
Measurements

	a-p	tr	a-p	tr
15977	P ² 7.1	4.0	dP ³ 8.5	6.7
14525	upper molar		6.0	6.8
15413	upper molar		6.8	7.8
15414	upper molar		7.0	7.6
15754	upper molar		8.4	9.8
19731	upper molar		8.3	10.8
15757	upper molar		8.6	11.9
16055	P ₂ 5.8	3.1	P ₃ 8.1	4.5

Family OROMERYCIDAE Gazin 1955

Gazin (1955:14 and 68) removed from the Camelidae the genera *Eotylopus*, *Camelodon*, *Protylopus*, and *Oromeryx* placing them in a new family, the Oromerycidae. At the same time, he described a new genus, *Malaquiferus*, assigning it to this family. This family was characterized as showing certain convergence to the camelids in the morphology of the lower premolars, the small canine and the procumbent lower incisors but in having strikingly different molar morphology. Also, all members of the Oromerycidae, as then known, were relatively short snouted forms with brachydont dentitions, not as slender limbed as the camelids and with separate metapodials.

Wilson (1974) disagreed with Gazin and reduced the Oromerycidae to a subfamily of the Camelidae, placing *Protylopus* as ancestral to *Poebrotherium*. Golz (1976:39–41) has recently thoroughly reviewed the taxonomic history of these genera and recognized the Oromerycidae as a distinct and possibly parallel group to the Camelidae. He suggests that *Poebrodon*, the earliest known camelid, may have



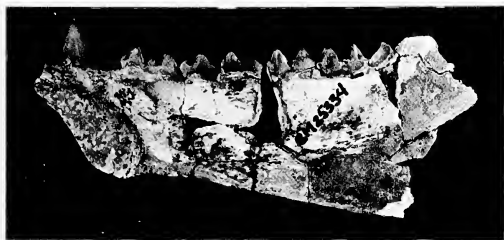
8



9



10



11

Figs. 8–11.—*Diplobunops matthewi*, all $\times 1/2$. 8) Dorsal view of mandible, USNM 20305. 9) Lateral view of same. 10) Dorsal view of right mandible, CMNH 25334. 11) Medial view of same.

Table 3.—*Statistical data on dentitions of Diplobunops matthewi from Badwater.*

Tooth and measurements	N	OR	M	SD	CV
P ¹ a-p	1		7.3	—	—
tr	1		4.3	—	—
P ² a-p	6	9.3–10.8	10.02	.496	4.95
tr	6	4.4– 6.2	5.6	.623	11.13
P ³ a-p	7	9.3–11.2	10.21	.727	7.12
tr	7	8.2–10.2	9.46	.787	8.32
P ⁴ a-p	11	7.1–10.9	9.67	1.18	12.20
tr	11	10.0–13.1	12.37	1.03	8.33
M ¹ a-p	9	10.3–12.3	11.39	.81	7.11
tr	10	12.0–15.0	13.70	1.21	8.83
M ² a-p	9	11.9–15.1	13.82	1.06	7.67
tr	9	14.2–18.1	16.49	1.49	9.04
M ³ a-p	6	13.3–15.5	14.50	.97	6.69
tr	7	15.7–18.6	17.71	1.32	7.45
dP ³ a-p	4	8.6–10.1	9.07	—	—
tr	4	6.7– 8.3	7.32	—	—
dP ⁴ a-p	3	9.0–11.5	10.00	—	—
tr	3	9.8–12.2	11.1	—	—
P ₁ a-p	3	8.4– 9.7	9.13	—	—
tr	3	6.1– 7.6	6.80	—	—
P ₂ a-p	9	7.8– 8.8	8.41	.407	4.84
tr	9	4.6– 5.1	4.73	.274	5.79
P ₃ a-p	15	8.1–10.5	10.7	.555	5.51
tr	15	4.5– 6.9	6.35	.479	7.54
P ₄ a-p	14	9.8–11.9	11.09	.635	6.00
tr	15	6.1– 8.8	7.54	.749	9.93
M ₁ a-p	19	9.1–12.0	10.69	.883	8.26
tr	19	7.2– 9.7	8.31	.758	9.12
M ₂ a-p	13	12.3–14.9	13.43	.865	6.44
tr	13	9.0–11.1	10.12	.608	6.01
M ₃ a-p	4	19.6–20.0	19.8	.231	1.17
tr	4	9.7–10.4	10.1	.294	0.40
dP ₄ a-p	5	11.5–13.0	12.24	.658	5.38
tr	5	6.0– 7.3	6.46	.522	8.08

evolved from a dichobunid line separate from that which gave rise to oromerycids. I agree with Golz that oromerycids do indeed appear to represent a distinct group of essentially late Eocene, partially selenodont, artiodactyls, which share certain characters with camelids (Fig. 1).

Although several oromerycids are known from the late Eocene of California and at least two, possibly three, from the earliest Oligocene of Texas, only one species of the family is recognized at present in the Badwater assemblages. *Malaquiferus tourteloti* is a specialized form, somewhat removed from the other members of the family. Its occurrence at Badwater is restricted to localities 5, 6, and 7 and Dry Creek, all of which produce a Uinta C equivalent fauna. *Malaquiferus* is not known from the younger Badwater faunas such as those from the Wood locality and locality 20.

Genus *Malaquiferus* Gazin, 1955

Type species.—*Malaquiferus tourteloti* (Gazin 1955:76).

Revised diagnosis.—Orbit large; snout short; cranium elongate; enamel of cheek teeth highly rugose; styles of upper molars weak, ribs strong; upper molars slightly oblique, approaching a square occlusal outline; small protoconule on M^1 - M^3 ; protocone only slightly bilobate; cheek teeth low crowned.

Type locality.—Section 11, T39N, R92W, 1½ mi northeast of East Fork of Dry Creek, Fremont County, Wyoming.

Age.—Uintan, late Eocene.

Distribution.—Only known from the type locality and from Badwater localities 5, 6, and 7.

Malaquiferus tourteloti Gazin 1955

Figs. 12–18

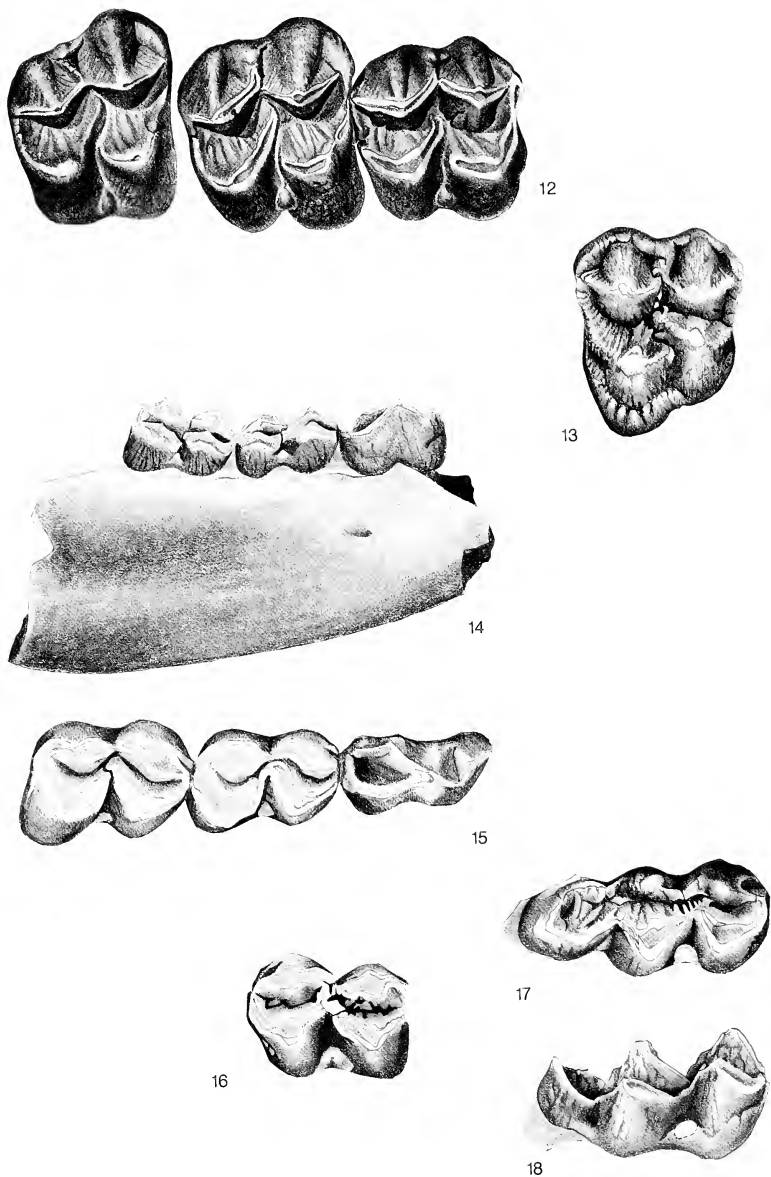
Holotype.—USNM 20588, greater part of a skull with $R + LP^4$ - M^3 .

Referred material.—CM 31395, LP^3 - P^4 ; 15987, LP^3 ; 15392, RM^1 - M^3 ; 14541, RM^2 - M^3 ; 18248, RM^2 - M^3 ; 14538, 14881, 15393, 15394, 15395, 15397, 15400, 15409, 15410, 13249, 18250, 19755, 19769, 29025, and USN, 21102, all isolated upper molars; 14438, RP_3 - P_4 ; RP_4 - M_2 ; 29497, LP_4 - M_1 ; 15983, 18247, 25327, 29496, 14536, isolated lower M_1 and M_2 ; 15396, RM_3 ; 14433, LM_3 .

Description.—The enamel on all the cheek teeth is quite wrinkled. The teeth are relatively low crowned and are bunoselenodont.

P_3 is elongate and rather narrow. The enamel is wrinkled. The parametacone is the only distinct cusp with both the parastyle and metastyle indistinct. There is a low ridge-like internal shelf with some swelling in the protocone position.

P^4 is broader transversely than anteroposteriorly, more so than in *Protylopus* and *Eotylopus*. The tooth has three roots and is rather acutely triangular. The parastyle and metastyle are only moderately developed. The parametacone is undivided and bears a slight rib down its buccal face. The protocone is sharply conical and somewhat smaller than the parametacone. The cusps are more bunodont than those of *Protylopus* more as in *Merycobundon littoralis*. P^4 is more anteroposteriorly compressed than in *Merycobundon*. The anterior crest from the protocone connects with the parastyle; the posterior crest is short, low, and quite wrinkled. It terminates below the posterointernal corner of the parametacone or the posterior cingulum. The posterior cingulum is long, while the anterior cingulum is restricted to a very small protruberance on the anterior face of the protocone.



Figs. 12-18.—*Malaquiferus tourteloti*. 12) CMNH 15392, RM¹-M³, ×3. 13) CMNH 14881, left upper molar, ×3. 14) CMNH 19737, RP₄-M₃, lateral view of mandible fragment, ×2. 15) Same occlusal view RP₄-M₂, ×3. 16) CMNH 18247, LM₁, ×3. 17-18) CMNH 15396, RM₃, ×3.

The upper molars are of approximately equal size, M^1 slightly smaller than M^2 and M^3 . The metacone on all is set somewhat internal to the paracones with the parastyles projecting buccally. However, particularly when worn, the molar occlusal outline is essentially square. The cusps are somewhat sharper than in *Merycobunodon* but not as selenodont as those of *Protylopus* and *Eotylopus*. There is some variation in the upper molars as to the degree in which the enamel is wrinkled. It is much more deeply wrinkled and pitted on the Badwater specimens than on the type (USNM 20588) from Dry Fork some 20 mi to the west.

The parastyle and mesostyle are prominent but low on M^1 - M^3 , whereas the paracone and metacone ribs are very strong on all molars. The metastyle is present on some teeth (CM 14551) and absent on others (CM 15392). The lingual cusps are moderately crenate, whereas the labial ones are essentially conical with straight anteriorly and posteriorly directed crests, which form a nearly straight ectoloph.

A small protoconule (paraconule of Golz), situated on the anterior flank of the protocone somewhat below its apex, is also present on all upper molars. A short crest descends steeply from the protoconule to the parastyle. A posterior crest from the protocone is weakly but broadly bifurcate on all the upper molars. On all specimens there is a deep and quite narrow valley between the posterior protocone crest and the anterior crest of the metaconule, which drops steeply while passing labially to fuse with the reduced metastyle. A very short anterior cingulum is generally present on M^1 - M^3 but may be absent on M^3 (CM 15392). There is no strong internal cingulum as is seen on molars of *Merycobunodon* and to a lesser extent on *Protylopus*. A distinct cusp, quite low, is generally present filling the valley between the protocone and metaconule.

The lower dentition of *Malaquiferus* has not been previously described. The lower premolars and molars all have wrinkled enamel, although it is generally not as coarsely developed on the lower teeth as on the uppers, except perhaps on M^3 . The teeth are mesodont with the molar cusps bunoselenodont.

P_3 and P_4 are transversely compressed with the protoconid as the dominant cusp. There is a short crest from the protoconid to a strong triangularly shaped paraconid. Posteriorly a crest drops from the protoconid to the rear of the tooth, turns lingually and terminates at the posterointernal corner where it is joined by a crest from the metaconid. A rather deep and broad talonid basin is enclosed between the two crests. The metaconid is not distinct, but is represented by a slight swelling on the crest, which passes posterointernally from the protoconid. A short, narrow anterior cingulum is present well down the paraconid face.

M_1 and M_2 are subequal in size and show essentially the same morphology. The anterior and posterior moieties remain separate until the teeth are well worn. The principal cusps are of about equal size, although the metaconid and entoconid are somewhat higher and sharper cusps on unworn teeth (CM 19583). There is no indication of lingual stylids on M_1 - M_3 . The anterior crests from the protoconid and metaconid fuse early in wear giving a rather rounded occlusal appearance to the anterior face of M_1 and M_2 . The posterior crest from the protoconid passes internally but, rather than fusing with the crests of the lingual border, turns sharply back labially and fuses with the anterior arm of the hypoconid. There is thus a continuous shallow central valley between the labial and lingual cusps. Such is not the case in *Protylopus* and *Eotylopus*. The entoconid on M_1 and M_2 remains separate from the metaconid almost throughout the life of the molars. The entoconid and hypoconid join posteriorly through a broad, curving crest. The anterior cingulum on M_1 and M_2 is greatly reduced. There is a strong, low cusp between the protoconid and hypoconid filling the buccal valley.

The morphology of M_3 is essentially the same as that of M_1 and M_2 but with the addition of a complex third lobe posteriorly. The anterior cingulum on M_3 is strong and passes from the buccal border across the anterior face and around the lingual face of the metaconid. The protoconid-hypoconid crests join internally and send a short spur

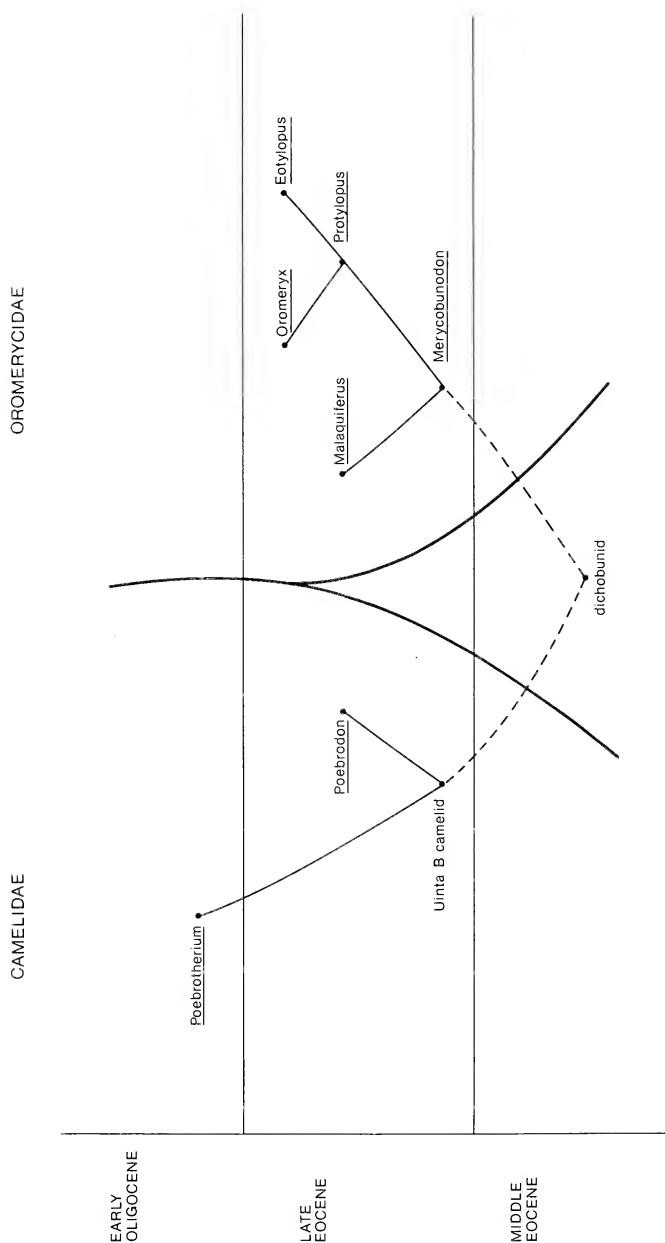


Fig. 19.—Suggested relationships of late Eocene Camelidae and Oromerycidae.

Table 4.—Statistical data on dentitions of *Malaquiferus tourteloti*.

Tooth and measurement	N	OR	M	SD	CV
P ⁴ a-p	1	5.8			
tr	1	6.5			
M ¹ a-p	4	6.1–6.8	6.45		
tr	4	6.8–7.8	7.40		
M ² a-p	10	7.0–7.8	7.45	.32	4.29
tr	10	7.9–9.4	7.73	.40	4.58
M ³ a-p	5	6.8–7.8	7.36	.48	6.52
tr	5	7.9–9.4	8.72	.55	6.32
P ₄ a-p	2	6.5–6.6	6.55		
tr	2	3.4–3.5	3.45		
M ₁ a-p	2	6.2–6.6	6.40		
tr	2	4.6	4.60		
M ₂ a-p	5	6.8–7.5	7.20	.33	4.58
tr	5	5.0–5.5	5.26	.19	3.61
M ₃ a-p	1	11.0			
tr	1	5.2			

into the posterior internal slope of the metaconid. The posterior hypoconid and entoconid crests pass directly posteriorly to form the complex posterior lobe. The basin of the posterior lobe is completely closed and is to a large extent filled and divided by a large central cusp. The lobe has a strong, distinct posteroexternal cusp and a smaller cusp at the rear of the entoconid.

A small portion of lower jaw is preserved (CM 19737), which shows that the mandible deepens from P₄ to M₃. A single mental foramina is preserved below the posterior half of P₄.

Discussion.—Golz (1976:39–41) provides a thorough review of the relationships of the members of the Oromerycidae. Of *Malaquiferus*, he says “*Malaquiferus tourteloti* of the Badwater fauna of Wyoming differs from other genera in relatively reduced styles and pronounced ribs on the upper molars. Its relationships to the other genera are not known.” On the basis of the much larger sample now available, I believe some suggestions as to its place in the family can be made.

Malaquiferus is primitive in the following characters: 1) displaying rather square and low crowned upper molars; 2) weak upper molar crests; 3) presence of protoconules on M¹–M³; 4) absence of stylids on lower molars; 5) weak crests on lower molars. The genus is specialized in the following characters: 6) the extreme wrinkling of the enamel of the cheek teeth; 7) prominence of ribs on M¹–M³; 8) absence of internal cingula on upper molars; 9) loss of hypocone; 10) bilobate posterior protocone crest; 11) subcrescentric metaconid and entoconid of M₁–M₃; absence of paraconid or parastylid; 12) some increase in crown height of lower molars.

In characters 1, 2, and 3, *Malaquiferus* resembles *Merycobunodon*, but it differs and appears more advanced in characters 6, 7, and 8. As no lower molars are known for *Merycobunodon* the two cannot be compared in other respects. *Malaquiferus* differs from *Protylopus* and *Oromeryx* in smaller size, having more nearly equal M^1 to M^3 , and in characters 1, 2, 5, 6, 7, and 8.

Malaquiferus would appear to be close to the dichobunid ancestry of the family in characters 1 through 5, but more advanced than the early Uinta *Merycobunodon* at least in the loss of internal cingula on the upper molars and in the degree of wrinkling of the enamel.

On this basis, I would suggest that *Malaquiferus* represents a relatively primitive oromerycid (Fig. 19) close to the point of origin of the family, possibly derived from *Merycobunodon*. Because of its highly wrinkled enamel and the loss of lingual upper molar cingula, I do not believe that *Malaquiferus* played any part in the ancestry of other oromerycid taxa.

Measurements in millimeters of teeth of *Malaquiferus tourteloti*

	P ₄		M ₁		M ₂		M ₃			
	a-p	tr	a-p	tr	a-p	tr	a-p	tr		
25327					6.9	5.2				
19737	6.5	3.5	6.2	4.6	6.8	5.4				
15396							11.0	5.2		
18247			6.6	4.6	7.5	5.5				
15983					7.5	5.2				
14536					7.3	5.0				
29497	6.6	3.4								
	P ³		P ⁴		M ¹		M ²		M ³	
15397							7.8	8.6		
18249							7.9	8.6		
18250							7.2	8.8		
18248							7.0	8.6	6.8	8.6
15395							7.3	8.8		
14538							7.2	8.5		
14541									7.8	8.7
14881							7.7	9.2		
29025									7.8	8.4
15395										
15392					6.5	7.2	7.2	7.9	6.9	7.9
19769					6.1	6.8				
19755							7.8	8.7		
19394					6.4	7.8				
31395	6.55	3.95	6.00	6.10						
USNM 20588			5.8	6.5	6.8	7.8	7.4	8.8	7.5	9.0

Family PROTOCERATIDAE Marsh, 1891

Subfamily LEPTOTRAGULINAE Zittel, 1893

Gazin (1955:17) placed three genera in the subfamily Leptotragulinae, two of which, *Leptotragulus* and *Leptoreodon*, are extremely difficult to differentiate one from the other. The third genus he included in this subfamily is *Poabromylus*. A fourth form, *Toromeryx*, recently described by Wilson (1974), should also be included here.

Leptotragulus is distinguished from *Leptoreodon* principally on characters of the lower premolars with almost no noticeable difference in the upper dentition or the lower M_1 to M_3 dentition. Likewise, the known skulls and postcranial material of the two genera are quite similar. Golz (1976:57) remarked on the great similarity of the two genera but refrained from synonymizing *Leptoreodon* with *Leptotragulus*, which has priority, having been described by Scott and Osborn in 1887. I, too, have retained both genera, although I believe that a thorough review of the now extensive collections referred to *Leptotragulus* and *Leptoreodon* would probably show them to be congeneric.

At present the two genera are separated on characters of P_3 and P_4 ; Gazin (1955:82) summarized these differences as follows: "In the lower jaws both P_3 and P_4 have an anterolingually directed crest from the protoconid, but in *Leptotragulus* the anterior extremity is more sharply flexed with a better-defined parastylid. A posteroexternal crest extends from the protocone, then swings inward forming the posterior crest of the heel. A posterointernal crest extends posteriorly and only slightly inward from the apex of the protoconid but terminates before reaching the posterior crest, leaving the talonid basin broadly open lingually. In some material of *Leptotragulus*, this talonid basin of P_4 may be partially constricted medially by a slight implication from the posterointernal crest. In *Leptoreodon* there is a prominent metaconid posterointernal to the protoconid in P_4 and apparently also in P_3 . Moreover, P_4 of *Leptoreodon* exhibits a usually distinctive, though variably developed, entoconid. In *Leptomeryx* the entoconid is well developed, and in P_4 joins the metaconid in early wear, but in P_3 joins the external crest well back of the protoconid."

In describing the California material, Golz (1976:57) noted some variation in these characters in specimens he assigned to species of *Leptoreodon*, although none of his examples of P_4 displayed either the weak metaconid or sharply flexed anterior crest of P_4 characteristic of *Leptotragulus*. In contrast most of the Badwater lower premolars show the *Leptotragulus* condition and only a relatively few have a large bulbous metaconid and the broadly flexed anterior crest on P_4 .

Therefore, I have assigned the majority of the Badwater specimens to *Leptotragulus medius* while assigning only specimens displaying a

large metaconid on P_4 to the genus *Leptoreodon*. Two species of *Poabromylus* also occur in the Badwater faunas.

Leptotragulus Scott and Osborn, 1887

Leptotragulus medius Peterson, 1919

Figs. 20, 21, 23, 25

Material.—CM 19733, RdP^4-M^3 ; 15984, RdP^3-dP^4 ; 29014, LM^1-M^3 ; 14592, 15974, P^4 ; 14437, 14468, 14471, 14542, 14584, 15401, 15404, 15408, 15975, 16755, 16758, 16784, 16797, 18255, 19758, isolated upper molars; USNM 21103, RP_3-M_1 ; USNM 21104, LP_4-M_1 ; CM 31392, LP_3-M_3 ; 23974, LP_3-M_1 ; 29049, M_1-M_2 ; 14540, 14593, 15584, P_2 ; 14539, RdP_3 ; 14594, LdP_3 ; 16040, 16760, P_3 ; 29059, LdP_4 ; 16757, 16759, P_4 ; 14431, 14470, 15402, 15406, 15411, 15412, 15976, 15978–15980, 19759, 19771, 31394, isolated lower first or second molars; 15986, RM_3 .

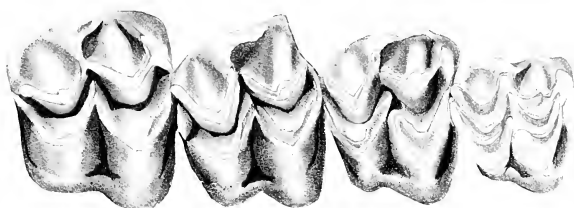
Description.—Much of the material consists of isolated teeth, although there are three maxillary fragments, which preserve deciduous upper molars and one almost complete jaw, CM 31392, from Dry Fork, which is badly broken and has quite worn molars. USNM 21103 and 21004 show the unworn P_4 together with M_1 .

The deciduous upper third molar is elongate and rather narrow, with the parastyle, paracone, and metacone strung out in a long anterior-posterior ridge. The protocone apex is set slightly in front of, and internal to, the metacone with short anterior and posterior lophs passing towards the metacone. The dP^4 is slightly more transverse than elongate and is slightly skewed. The styles are prominent and the ribs reduced. This tooth is essentially molariform but considerably smaller than M^1 . Permanent P^4 is quite simple and triangular in occlusal outline. The parametacone is undivided and short crests pass from it to the low para- and metastyles. The protocone is sharply crescentic with low anterior and posterior crests passing to the styles. Short, internally restricted cingula are present.

The upper molars display essentially the same morphology and increase in size from M^1 to M^3 . They are somewhat transverse with the protocone on each set more lingually than the metaconule. The parastyles and mesostyles are more prominent than the metastyles on M^1-M^3 . Both paracone and metacone ribs are developed with the paracone rib the stronger of the two. The posterior crest from the paracone is short and does not fuse with the mesostyle until the tooth is well worn. The protocone and metaconule are sharply crescentic. The anterior arm of the protocone and the posterior arm of the metaconule pass to the internal side of the parastyle and metastyle. In the midline, the posterior arm of the protocone passes buccally between the paracone and metacone while the anterior crest from the metaconule is shorter and directed more into the base of the protocone crest. The anterior cingulum is strong but the lingual and posterior cingula are variable and usually only weakly developed. The lingual valley between the protocone and metaconule is shallow and constricted and there is no pillar at its internal margin.

The deciduous third and fourth lower premolars are longer than their permanent counterparts and taper anteriorly. There is no distinct paraconid on dP_3 and the anterior crest is short, with the protoconid set near the anterior end of the tooth. A crest passes diagonally from the posterolingual side of the protoconid to the posterobuccal corner where a large hypoconid is present. Two crests pass lingually from the hypoconid, one to a small entoconid, the other along the posterior border of the tooth. DP_4 bears six primary cusps and has a small anteriorly projecting cuspule in the middle of the anterior lophid.

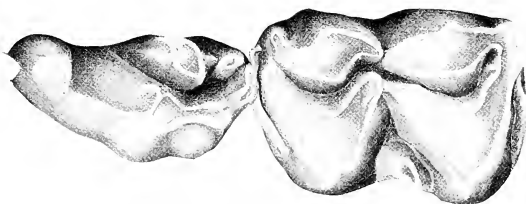
P_2 is elongate and quite compressed laterally. There is a distinct paraconid set at an angle to the anterior crest from the protoconid. Two crests pass posteriorly from the protoconid to the posterior border and they enclose a narrow valley between them. P_3



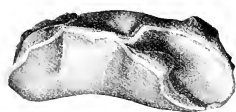
20



21



22



23



24



25

Figs. 20–24.—*Leptotragulus* and *Leptoreodon*. 20) *Leptotragulus medius*, CMNH 19733, RdP⁴-M³, $\times 3$. 21) *Leptotragulus medius*, USNM 21103, RP₃-M₁, $\times 5$. 22) *Leptoreodon* sp., CMNH 29374, LP₄-M₁, $\times 5$. 23) *Leptotragulus medius*, CMNH 16040, RP₃, $\times 5$. 24) *Leptoreodon* sp., CMNH 21105, LP₄, $\times 5$.

Fig. 25.—*Leptotragulus medius*, CMNH 16757, $\times 5$.

and P₄ are somewhat broader than P₂ with more expanded talonids. On both, the paraconid is distinct and set at an angle to the anteroposterior axis of the tooth. A strong buccal crest passes from the protoconid posteriorly to the posterobuccal corner but no distinct entoconid is present. A much shorter crest passes from the protoconid posterolingually but this crest never reaches the posterior border. The talonid basin is open along the posterolingual margin of P₃ and P₄. No metaconid is present on either P₃ or P₄.

The lower molar cusps are quite sharp and high and the teeth increase in length from M_1 to M_3 . There is almost no trace of ribs on the metaconid and entoconid, and the parastylid is weak. The crests of the metaconid and entoconid are nearly straight but overlap slightly at the middle of the lingual margin. The median labial shelf is narrow and generally bears a small cuspule. The posterior arm of the hypoconid is strong and terminates behind the entoconid in a heavy ridge. The anterior and posterior cingula are moderately developed. M_3 has essentially the same structure as M_1 and M_2 with the addition of the third lobe. The basin of the posterior lobe is cut off from the basin between the hypoconid and entoconid by a strong crest.

Discussion.—This sample *Leptotragulus medius* is quite similar to that from the Uinta Basin. The divergent protoconid crests on P_3 and P_4 are particularly characteristic of this species (Gazin, 1955:85). A review of all material of both *Leptotragulus* and *Leptoreodon* is now needed to determine relationships in this subfamily.

Measurements of teeth of *Leptotragulus medius*

	dP ³		dP ⁴		M ¹		M ²		M ³	
	a-p	tr	a-p	tr	a-p	tr	a-p	tr	a-p	tr
CM 15984	6.15	4.00	5.35	5.65						
19733			5.40	5.65	5.90	7.05	6.40	8.30	7.10	8.60
29014					5.40	7.60	6.20	8.30	6.80	8.30
18208			5.30	—						
16758					6.00	6.80	6.80	8.35		
	P ³		P ⁴		isolated upper molars					
15987	6.45	4.25	5.90	6.80						
14592			5.10	6.30						
15974										
14437							6.50	8.60		
14438							6.60	8.50		
14542							7.00	8.40		
14584							6.60	8.50		
14685							7.10	8.90		
15401							7.90	8.65		
15404							6.85	9.10		
							a-p	tr		
15408							6.20	7.10		
15975							6.20	7.60		
16755							6.75	8.35		
16784							7.25	8.60		
16797							7.30	8.70		
18255							6.70	7.50		
19758							6.05	7.80		
	P ₂ -M ₃		P ₂ -P ₄		M ₁ -M ₃					
	a-p		a-p		a-p					
CM 31392	39.80		15.80		23.70					

	P ₃		P ₄		M ₁		M ₂		M ₃	
	a-p	tr	a-p	tr	a-p	tr	a-p	tr	a-p	tr
31392	5.40	2.65	5.90	3.30	6.05	5.40	6.80	5.90	10.75	5.90
USNM 21103	5.50	2.60	6.10	3.45	6.75	5.10				
15986									9.95	5.75
	P ₂		P ₃		P ₄					
14540	5.10	1.90								
14593	5.20	2.30								
15584	5.20	1.90								
14438			5.75	3.00	6.05	3.50				
14539			6.00	3.30	deciduous					
14594			5.60	3.00	deciduous					
16760			6.20	2.90						
16757					5.75	2.85				
16759					6.15	2.90				
29059					7.30	3.60	deciduous			
	isolated lower molars									
							a-p	tr		
14431							7.30	5.40		
14470							6.05	4.50		
15402							6.60	5.20		
15406							7.10	5.65		
15411							5.90	4.95		
15412							5.90	4.60		
15976							6.45	5.10		
15978							6.80	5.60		
15979							6.35	5.20		
15980							6.60	5.15		
19759							6.95	5.30		
19771							7.40	5.10		
31394							6.60	5.20		

Leptoreodon Wortman, 1898

Leptoreodon sp.

Figs. 22, 24

Material.—USNM 21105, LP₄; CM 29374, LP₃-M₁; 14432, LP₄; 19734, RP₄.

Description.—The only specimens, which can be assigned to *Leptoreodon*, are those which preserve P₄. The lower M₁ in CM 29347 is indistinguishable from lower molars of *Leptotragulus medius*. The fourth lower premolars all have a robust metaconid and distinct ridge which runs from the metaconid to the rear of the tooth and which closes the talonid basin internally.

Measurements of teeth of *Leptoreodon* sp.

	P ₃		P ₄		M ₁	
	a-p	tr	a-p	tr	a-p	tr
CM 23974	5.60	2.45	5.90	3.60	6.60	5.10
14432			5.75	3.20		
19734			5.75	3.20		
21105			5.90	3.70		

Poabromylus Peterson 1931**Poabromylus golzi**, new species

Figs. 26-29

Holotype.—CM 25448, RP⁴-M³.*Hypodigm*.—Type and CM 29049, RP₂-P₃, M₁-M₂.*Locality*.—Badwater locality 20.

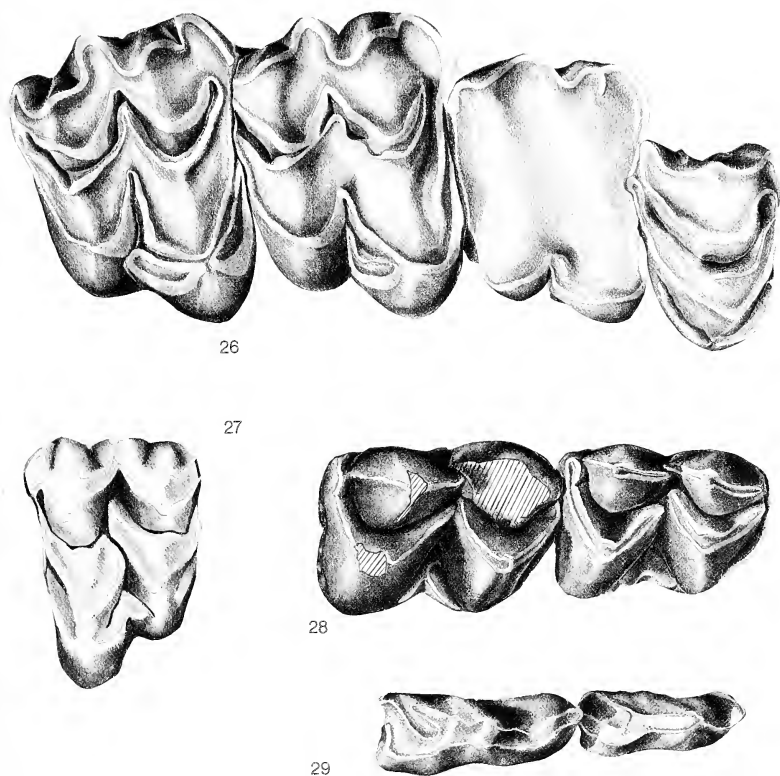
Diagnosis.—Smaller than *Poabromylus kayi*; cheek teeth lower crowned; enamel not as thick as in *Heteromeryx*; teeth higher crowned, more selenodont than in *Toromeryx*; internal cingulum complete on P⁴, reduced on M¹-M².

Etymology.—Named for David J. Golz who has recently reviewed the California late Eocene artiodactyls.

Description.—P⁴-M³ are distinctly wider than long, more pronouncedly so than in *Leptotragulus*. On P⁴ the parastyle and metastyle are strong and project buccally. The parametacone is undivided. The lingual cusp is V-shaped and sends crests buccally to fuse with the styles. A cingulum is complete on P⁴ from the anterior face around the inner cusp onto the posterior side of the tooth.

M¹ is so worn that all occlusal detail is obliterated. M² and M³ have strong anterobuccally projecting parastyles prominent mesostyles and on M³ a distinct mesostyle. The paracone and metacone are crescentic. The valleys between the paracone and protocone, and metacone and metaconule are fairly deep, more so than in *Heteromeryx*. The posterior crest from the protocone and the anterior crest from the metaconule pass buccally and fuse between the paracone and metacone. The anterior crest from the protocone passes externally to fuse with the parastyle and the posterior metaconule crest fuses with the metastyle on M³ while on M² it terminates at the posterointernal corner of the metacone. The anterior and posterior cingula on M¹-M³ are greatly reduced to absent; there is no buccal cingulum as in *Heteromeryx*. The internal cingulum between the protocone and metaconule is small.

In the lower dentition there is a diastema between P₁ and P₂ and from the shape of the alveolus P₁ was caniniform. P₂ and P₃ are elongate, narrow teeth, neither having a metaconid. From the protoconid a crest runs anteriorly to a distinct paraconid, which is set slightly to the internal side of the tooth. On both P₂ and P₃ the posterior crest from the protocone bifurcates, sending a narrow crest posterointernally and a stronger crest directly posteriorly to the end of the tooth. The internally directed crest does not reach the posterointernal corner of either P₂ and P₃. There is no distinct entoconid nor talonid basin. M₁ and M₂ are moderately high crowned with the labial cusps distinctly crescentic. The lingual cusps are sharp and the metaconid and entoconid have very short anterior and posterior crests and do not fuse into a lingual lophid until late in wear. The anterior crest from the protoconic terminates below the anterointernal corner



Figs. 26–29.—*Poabromylus golzi*. 26) CMNH 25448, RP^4-M^3 , $\times 3.5$. 27) CMNH 14474, LM^2 , $\times 3$. 28–29) CMNH 29049, RP_2P_3 , M_1-M_2 , $\times 3.5$.

of the metaconid; there is no stylid present. The posterior crest from the hypoconid passes to the lingual border terminating behind the entoconid. The anterior cingulum stretches across the entire anterior face of M_1 and M_2 . The external valley is deep and is filled at the buccal margin by a low pillar.

Measurements of teeth of *Poabromylus golzi*

	P^4		M^1		M^2		M^3	
	a-p	tr	a-p	tr	a-p	tr	a-p	tr
CM 15248	5.60	7.25	7.20	9.25	8.10	10.75	8.50	10.55
	P_2		P_3		M_1		M_2	
CM 29049	5.90	2.30	7.00	2.85	7.50	5.45	8.10	6.30

Poabromylus cf. *P. golzi*

CM 14474	7.65	10.90
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Discussion.—This species is referred to *Poabromylus* rather than *Leptoreodon* because of the absence of lower molar stylids, the even, broad crescentic selenes of M_1 - M_2 and the greater anterior transverse width than posterior in the upper molars. Also, the cingula of the upper molars are greatly reduced as they are in material referred to *Poabromylus kayi* by Wilson (1974: Fig. 13); upper molar cingula in *Poabromylus* are more reduced than in most *Leptoreodon* species.

Poabromylus golzi is smaller than *P. kayi* of the LaPoint. The latter is known only from a badly damaged lower jaw with P_3 to M_3 .

Poabromylus cf. *P. golzi*

Fig. 27

Referred material.—CM 14474, LM², from locality 7.

Description.—A single tooth from locality 7 is quite similar to the specimen from locality 20 but differs in having a much shorter posterior protocone crest and stronger anterior, posterior and internal cingula.

Family Leptomerycidae Scott, 1899

Hendryomeryx, new genus

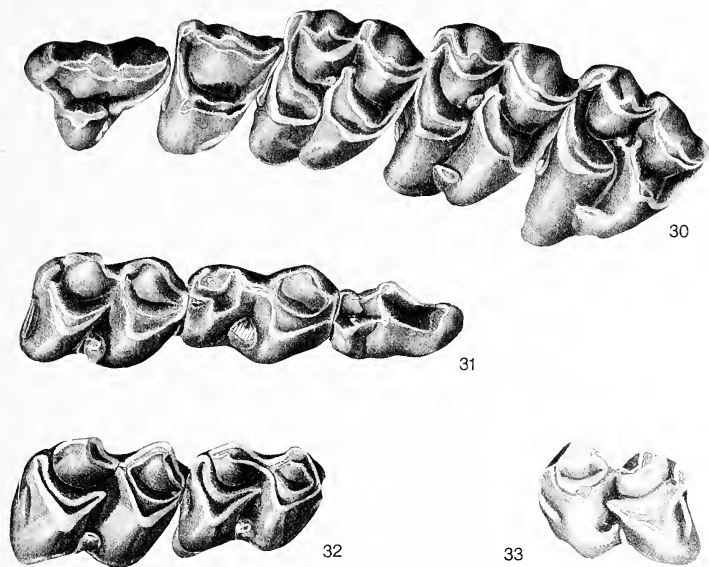
Type species.—*Hendryomeryx wilsoni*.

Generic diagnosis.—Protoconule absent on M^1 - M^3 ; all styles on M^1 - M^3 present but narrow; paracone rib developed on M^1 - M^3 , no metacone rib; posterior protocone crest very short, directed towards metaconule; P_4 talonid complex, enclosed; stylids on lower molars reduced or absent; selenes moderately developed on M_1 - M_3 ; entoconid and metaconid connected through a straight lingual crest.

Included species.—*Hendryomeryx wilsoni*; *Leptomeryx defordi* Wilson (1974:30); *Hendryomeryx* new species, unpublished from McCarty's Mountain, Montana (specimens in the Carnegie Museum collections).

Etymology.—Named for the Hendry family and the Greek *meryx*, ruminant.

Discussion.—*Hendryomeryx* is less advanced than the Oligocene *Leptomeryx* of the plains and intermontaine regions in having lower crowned, less selenodont molars, and a weak metaconid-entoconid lophid. *Hendryomeryx* is distinct from *Simimeryx* in the absence of the protoconule, presence of a mesostyle, in being somewhat more selenodont and in having more complex lower premolars. It has been suggested (Stock, 1934; Gazin, 1955; Golz, 1976) that *Simimeryx hudsoni* may be ancestral to *Hypertragulus* and that *Leptomeryx* be included with them in the family Hypertragulidae (Wilson, 1973). The lower premolars of *Simimeryx* are quite simple, much more so than in any of the *Hendryomeryx* species. In this respect *Simimeryx* is much closer to *Hypertragulus* than to *Hendryomeryx* and *Leptomeryx* and the latter two genera are hence placed in the Leptomerycidae.



Figs. 30–33.—*Hendryomeryx wilsoni*. 30) CMNH 29120, LP³-M³, ×3.5. 31) CMNH 29013, RP₄-M₂, ×3.5. 32) CMNH 29050, RM₁-M₂, ×3.5. 33) CMNH 18258, ×4.

Hendryomeryx wilsoni new species

Figs. 30–32

Holotype.—CM 29102, LP³-M³.

Hypodigm.—Type and CM 31391, RdP⁴-M¹, 31393, LdP⁴-M¹; 29056, RP²; 29054 RdP³ 29023, 29060, P³; 29013, RP₄-M₂; 29050, RM₁-M₂; 29044, LP₂; 29035, RM₁.

Locality.—All from Badwater locality 20.

Diagnosis.—Smaller, less high crowned molars than *Hendryomeryx defordi*; lower molars not as selenodont as in that species.

Etymology.—Named for John A. Wilson who has done extensive work on the Texas Eocene and Oligocene artiodactyls.

Description.—The type maxilla (CM 29120) shows slight wear on P³-P⁴, moderately worn M¹ and light wear on M²-M³. No P² is associated with the type, but an isolated P² (CM 29056) is assigned to the species. P² is three rooted but there is no internal median cusp. The paracone is sharp and sends crests directly anteriorly to a large parastyle and directly posteriorly to the end of the tooth. No metacone or metastyle is present. A narrow internal cingulum runs from below the paracone posteriorly to the rear of P². There are shallow concavities on the buccal face of P² before and behind the paracone.

P³ on the type has the paracone and parastyle set close together. There is a slight indication of a metacone behind the paracone, but it is not large, and the posterior crest from the paracone passes through it to the posteroexternal corner of the tooth. The internal cusp is quite large on P³ and connects to both the parastyle and the posteroexternal corner through low, thin ridges.

On P^4 the paracone is high and sharp with no indication of a metacone. The parastyle is quite small and low and there is no distinct metastyle. The internal cusp is crescentic with low but prominent anterior and posterior crests which pass to the parastyle and the posterorexternal corner. Very short narrow anterior and posterior cingula are present on P^4 near the internal base of the internal cusp.

The upper molars are essentially identical in structure, with M^1 somewhat smaller than M^2 and M^3 . On all molars the parastyle and mesostyle are compressed but distinct and the metastyle while present is smaller. There is a prominent rib on the paracone on M^1 - M^3 , but no distinct metacone rib. The anterior crest from the protocone terminates at the parastyle and carries a short, narrow anterior cingulum below the apex of the protocone. The posterior arm of the protocone is indistinct with the posterointernal face sloping off towards the metaconule. A deep, narrow valley separates the protocone from the metaconule and anterior crest of the metaconule. The latter passes buccally to terminate between the paracone and metacone. There is a distinct small pillar between the interior face of the paracone and the end of the anterior crest from the metaconule which, with wear, fuses with the crest forming a spur into the slope of the paracone. The posterior crest from the metaconule passes buccally to terminate at the posterointernal base of the metacone. There is no posterior cingulum on M^1 - M^3 . On all M^1 of CM 31391 there is a very faint suggestion of a remnant of the protoconule given by a shallow groove down the internal face of the anterior crest of the protocone also on this specimen dP^4 is preserved. The tooth is essentially molariform displaying, on a smaller scale, the same features seen on M^1 .

P_2 is elongate and quite narrow. It is rather complex with a distinct protoconid and metaconid the latter lying directly internal to the protoconid. The paraconid is large and the protoconid crest to the paraconid bends sharply internally. There is no posterior crest from the metaconid and hence no enclosed talonid basin. A crest passes directly posteriorly from the protoconid to the rear of the tooth. There is no distinct entoconid.

P_3 is not known. P_4 is quite complex with the protoconid and metaconid of equal size. An anterior crest descends steeply to the low parastylid which is set at a sharp angle to the crest. Posterior crests pass buccally from the protoconid to a distinct hypoconid and from the metaconid to a distinct entoconid. These crests enclose a narrow, deep talonid basin which is closed posteriorly by a high hypoconid-entoconid crest. A very narrow, short cingulum is present on the buccal face below and behind the parastylid.

M_1 and M_2 are rather low crowned, more so than in *Hendryomeryx defordi*. The metaconid and entoconid are sharp and project above the protoconid and hypoconid. There are no stylids on M_1 or M_2 . The anterior crest of the entoconid fuses with the posterior crest of the protoconid. The anterior crest of the hypoconid passes anterointernally to merge into the lower slope of the posterior protoconid crest. The posterior crest of the entoconid terminates at the posterointernal corner of M_1 and M_2 . No anterior cingulum is present on M_1 , but a very short narrow cingulum is present on both M_1 and M_2 . The buccal valley is closed by a low pillar on both M_1 and M_2 . In CM 29013 M_1 is somewhat aberrant with the hypoconid and entoconid essentially fused with a V-shaped valley between them.

Discussion.—*Hendryomeryx wilsoni* is quite distinct from any of the other selenodont artiodactyls in the Badwater faunas. It closely resembles *Hendryomeryx defordi* (Wilson) from the Porvenir fauna of west Texas. The latter is somewhat larger and slightly higher crowned than *H. wilsoni*. In the McCarty's Mountain fauna in Montana an undescribed species of *Hendryomeryx* appears to be present (CM 1057 and 31397) together with a species of *Leptomeryx*. The latter is higher

Measurements of teeth in *Hendryomeryx wilsoni*

	P ²		P ³		P ⁴		M ¹		M ²		M ³	
	a-p	tr	a-p	tr	a-p	tr	a-p	tr	a-p	tr	a-p	tr
CM 29120			5.15	3.90	3.30	5.00	5.10	5.80	5.30	5.80	5.35	6.80
CM 31391			deciduous		4.50	4.70	5.10	5.80				
31393			deciduous		4.65	5.60	5.80	6.65				
CM 29056	5.01	2.55										
CM 29023			5.40	3.95								
CM 29060			4.75	3.20								
29054			6.60	4.90								
					deciduous							

Hendryomeryx cf. *H. wilsoni*

	M ¹		M ²	
	a-p	tr	a-p	tr
CM 29498				
CM 29499				
CM 18205	4.80	4.85	<u>5.80</u>	6.45
	M ²		M ²	
	a-p	tr	a-p	tr
CM 18258				
CM 16021				

crowned, larger, and more selenodont. The early Oligocene leptomerycines need to be thoroughly restudied, but it appears likely that they evolved from *Hendryomeryx*. *Hendryomeryx defordi* (Wilson) from the Porvenir fauna of Texas is somewhat larger and slightly higher crowned than *H. wilsoni* and may well have evolved from that species.

The origin of *Hendryomeryx* within the dichobunids is unclear. No known early Uintan or late Bridgerian form appears at present to be a more likely ancestor than any other.

Hendryomeryx cf. *H. wilsoni*

Fig. 33

Material.—CM 29499, RM¹; 29498, RM²; 18025, RM₁; 16021, RM₁ or ₂; 18258, LM₁ or ₂.

Locality.—Wood and Rodent localities.

Description.—These specimens are all quite similar to material described for *Hendryomeryx wilsoni*. The lower molars are somewhat lower crowned with the hypoconid selene perhaps less crescentic. In other features they are essentially identical to the specimens from locality 20.

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ARTICLE 11

A NEW SPECIES OF AQUATIC *ANOLIS* (SAURIA, IGUANIDAE) FROM HISPANIOLA

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ABSTRACT

A new species of Alpha section aquatic *Anolis* is described from northern Haiti on the West Indian island of Hispaniola. Comparisons of the new species with its Beta section mainland aquatic relatives, as well as with the Cuban Alpha section *A. vermiculatus*, are made. The habitat and ecology of the type-locality are discussed in detail, and the coloration of the dewlap and its significance are postulated.

INTRODUCTION

Schwartz and Thomas (1975) listed 30 native and two introduced species of the iguanid lizard genus *Anolis* from the Antillean island of Hispaniola. One additional species has been described since 1975. Of these species, one (*A. brevirostris* Bocourt) is known to be composed of at least three sibling species (Webster and Burns, 1973) that remain unnamed. Williams (1977) pointed out the futility of now attempting to answer the basic question "How many species?" in the genus *Anolis*; the answer remains uncertain for a variety of reasons (see also Williams, 1976a), not the least of which are more ready accessibility of some areas and more careful and detailed collecting. The island of Hispaniola demonstrates these phenomena more strongly than any other of the West Indies.

I have summarized elsewhere (Schwartz, 1973) the striking number of new species of *Anolis* described from Hispaniola. As of 1977, 13

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new species have been described since 1960 as follows: *alumina* Hertz, *barahonae* Williams, *christophe*i Williams, *dolichocephalus* Williams, *fowleri* Schwartz, *insolitus* Williams and Rand, *koopmani* Rand, *marcanoi* Williams, *rimarum* Thomas and Schwartz, *rupinae* Williams and Webster, *sheplani* Schwartz, *singularis* Williams, and *whitemani* Williams. This listing is pertinent in that it includes anoles from a variety of habitats and with a variety of relationships. Six may appropriately be considered siblings of better known species: *alumina*, *barahonae*, *dolichocephalus*, *marcanoi*, *rupinae*, and *whitemani*. Nine may be considered upland or forest-dwelling species: *barahonae*, *christophe*i, *dolichocephalus*, *fowleri*, *insolitus*, *koopmani*, *rupinae*, *sheplani*, and *singularis*. One is an inhabitant of boulder jumbles (*rimarum*) and another of arid lowland desert (*whitemani*). Two are primitive (*insolitus*, *sheplani*). Five are known only from one or a very few localities (*fowleri*, *koopmani*, *rimarum*, *rupinae*, *sheplani*), whereas five are relatively widespread geographically (*alumina*, *dolichocephalus*, *insolitus*, *singularis*, *whitemani*).

The West Indian island of Hispaniola is customarily divided into two major segments, corresponding to the two paleoislands that were separated by a seaway that is now the Cul de Sac-Valle de Neiba plain—the north and south islands. Of the 13 newly named species of *Anolis*, five (*alumina*, *barahonae*, *dolichocephalus*, *koopmani*, *rupinae*) are restricted to the old south island (where none of them is truly widely distributed) and six (*christophe*i, *fowleri*, *insolitus*, *marcanoi*, *rimarum*, *whitemani*) are either restricted to the north island or have the major portion of their distributions there (*whitemani*, the exception, occurs in the Cul de Sac-Valle de Neiba plain but is also broadly, but apparently disjunctly, distributed over xeric areas on the southern and western portions of the north island). Two species are somewhat anomalous—*sheplani* occurs primarily in the south island Sierra de Baoruco but has been taken in the north island Sierra de Neiba, the range that forms the southern border of the north island, and where presumably it is a relatively recent invader, and *singularis* is widespread on the south island but it (or a close relative) occurs in the north island Sierra Martín García, an eastern affiliate of the Sierra de Neiba, and on Ile de la Gonâve. Thus, of the 13 newly named species, seven may appropriately be considered south island in affinities and six are north island lizards.

One niche that Antillean anoles have been unsuccessful in invading is that of streams or rivers. Only on Cuba is there an aquatic anole, *A. vermiculatus* Duméril and Bibron. This species has a relatively limited distribution in the western province of Pinar del Río. In small rivers and creeks, especially those passing through shrubby or wooded situations, *A. vermiculatus* is a relatively common lizard. The presence

of streamside shrubby growth and low trees and saplings are important for *A. vermiculatus*, because it sleeps on these plants. Large rocks and boulders are not necessary for its success, and the lizard may be common along placid streams. *A. vermiculatus* is not limited to only high elevations in Pinar del Río Province but occurs near sea level, provided streams with the proper sleeping sites exist. During the day, when the lizards are disturbed, they plunge into the water and go to the bottom where their cryptic browns and dull blues and greens act as almost perfect camouflage.

Elsewhere, on the Central and South American mainland, there are five species that are stream-associated—*barkeri* Schmidt, *aquaticus* Taylor, *lionotus* Cope, *poecilopus* Cope, and *macrolepis* Boulenger. These species extend from southern México (Oaxaca and Veracruz) to Colombia. Habits and habitat, as well as some meristic data for these species can be found in Taylor (1956), Robinson (1962), Meyer (1968), and Campbell (1973). The latter author gives a comprehensive summary of the literature on the mainland species (except *A. macrolepis*).

Thus, a total of six species of the huge genus *Anolis* are known to have been successful in occupying a niche that appears to be broadly open throughout much of the range of the genus. As Williams (1976a; 1977) pointed out, mainland anoles are much less well known than those of the West Indies, so it is likely that additional aquatic anoles will be found on the mainland. If these mainland species are restricted geographically or altitudinally, then it will be mere chance that they are discovered. Although the Antilles have been known to have a single aquatic species in Cuba, it seemed very unlikely that there might be another aquatic anole on these islands.

On 2 August 1977, while returning from Carrefour Marmelade and on the main road between Plaisance and Limbé in the western portion of the Massif du Nord in northern Haiti, Eugene D. Graham, Jr., Thomas M. Thurmond, and I stopped at a boulder-strewn stream in the late afternoon (about 1630 h). Our objective was to look over the stream as a prospective place for night-collecting of frogs. The stream, in an open ravine perhaps 6 m wide, is at a place known locally as Roche Parfait; although one might not appropriately consider this a torrential stream, still it rushes down a steep slope. Its banks and the stream bed are littered with boulders and rocks of various sizes, some as large as 2 or 3 m or even larger in diameter (see Fig. 1). The newly constructed road, at this point, did not utilize the old road with its culvert and bridge, so that there is, just to the west of the main road, a U-shaped curve with a culvert. The new road has a larger culvert, and the stream then proceeds down a steep slope to the Rivière du Limbé below. The area is remarkable for two reasons—there are no



Fig. 1.—View of the type-locality of *Anolis eugenegrahami*, from a Kodachrome transparency by Eugene D. Graham, Jr. The view is from the vicinity of the old culvert upstream, and the waterfall can be seen in the upper left.

human inhabitants in the immediate vicinity of the stream, and there is relatively luxuriant gallery forest, with bromeliads, ferns, shrubs, mosses, and lichens. Because so many streams in Haiti have houses adjacent to them and have had most of their gallery forest removed, this particular stream seemed exceptionally intriguing for frog collecting.

Graham and Thurmond ascended the stream as far as they were conveniently able. About 305 (linear) m above the road, there is a vertical waterfall ending in a shallow pool. An almost vertical path ascends the slope adjacent to the waterfall, but they did not (nor did we later) ascend this path. Upon returning to the automobile, they commented that they had seen many very dark anoles on the bank of the pool at the foot of the waterfall and on the boulders in the stream. When disturbed, the lizards sought refuge under wet boulders in the stream and in indentations behind the waterfall, never outside the stream margins. The lizards were very active on the rocks. One male was seen on a log fallen into the stream; this individual jumped off the log and scurried upstream on the rocks. I asked them whether these dark anoles might be one of the three abundant and widespread north island species—*A. cybotes* Cope, *A. distichus* Cope, or *A. chlorocyanus* Duméril and Bibron. None of these is “normally” black or seeks refuge in aquatic situations. However, despite the fact that *A. chlorocyanus* is customarily bright green, it does show a very dark brown to almost black phase. Because it is a shade-dwelling species, and the ravine is shaded, *A. chlorocyanus* seemed the most likely candidate for the lizards Graham and Thurmond had seen. The situation was equivocal but remained temporarily unresolved.

On the night of 4 August 1977, between 2200 and 2400 h, we visited the stream to collect frogs. We had already been collecting since 1930 h near Carrefour Marmelade in the uplands of the Massif du Nord and were on our way to Cap-Haïtien, when we decided to try for frogs in the Roche Parfait stream. Within 30 m of the old culvert, I stopped to relax in midstream for a minute or two against a large boulder. I felt something alive underneath my shirt and involuntarily brushed at it and then proceeded upstream. Immediately around the sharp corner of the boulder against which I had rested, I saw a large dark sleeping anole which was unfamiliar, and collected it.

With the knowledge that we had discovered a new anole, we concentrated on securing additional specimens and succeeded in finding 16. The lizards were not uncommon and were easily seen from about 10 m above the old culvert as far as the waterfall. On a second visit on 5 August, we found seven more, all associated with the stream and its boulders (although see comments below). Thus, a total of 23 specimens (10 males, 13 females), both adults and juveniles, of this new

species are available for study. In honor of one of the co-discoverers of this new species, I take very great pleasure in naming and describing it.

DESCRIPTION

Anolis eugenegrahami, new species

Holotype.—Carnegie Museum (CM) 60515, an adult male, from Roche Parfait, 9.0 km NE Plaisance, 215 m, Département du Nord, Haiti, one of a series collected on 4 August 1977, by Eugene D. Graham, Jr., Albert Schwartz, and Thomas M. Thurmond. Original number Albert Schwartz Field Series (ASFS) V45823.

Paratypes.—ASFS V45840-46, same locality and collectors as holotype, 5 August 1977; American Museum of Natural History (AMNH) 115515-16, CM 60516-18, Museum of Comparative Zoology (MCZ) 132384-87, National Museum of Natural History (USNM) 197326-29, same data as holotype.

Definition.—An aquatic species of *Anolis* characterized by the following combination of characters: size moderate (males to 72 mm, females to 61 mm snout-vent lengths); moderately sexually dichromatic, males black to greenish black dorsally, females black but mottled greenish laterally and with a middorsal series of four gray ovate blotches extending onto the dorsal side of the yellowish green tail; dewlap in males relatively small, black to dark gray centrally, edged whitish to very pale yellow; a narrow pale yellowish subocular semicircle; nape pattern (clearest in females and juveniles, much obscured in males) of a dark-edged hollow "collar;" upper surface of head randomly vermiculate with black on an olive to gray ground; juveniles with a green flank stripe, absent in adults of both sexes; snout scales at level of second canthal scale 12 to 15; scales between supraorbital semicircles two to four; scales between supraorbital semicircles and interparietal scale tiny, from six to 10; 13 to 18 scales around small interparietal; four to eight postrostral scales; dorsal scales tiny, with about four middorsal longitudinal rows elongate and smooth to very weakly keeled, all other dorsal scales tiny and almost granular, 40 to 56 middorsals in snout-ear distance; ventral scales small, smooth, 37 to 63 in snout-ear distance; canthal scales three to six, with the most anterior ones not larger than adjacent scales; always one row of scales between the subocular scales and the supralabial scales; five to seven postmental scales; femur length/snout-vent length ratio 30.1 to 32.2 in males, 28.6 to 32.3 in females (all sizes combined).

Distribution.—Known only from the type-locality.

Description of the holotype.—An adult male with a snout-vent length of 72 mm and tail length of about 130 mm, distal half regenerated; snout scales at level of second canthal scales 12, six rows of loreal scales, supraorbital semicircles separated by three rows of scales, eight scales on each side between the interparietal scale and the su-

praorbital semicircles, 16 tiny scales around interparietal scale, about 11 enlarged scales in supraocular disk, median dorsal scales in snout-anterior border of ear distance 44, ventrals in snout-ear distance 48, supralabial scales separated from subocular scales by two rows of scales, six postmental scales, six scales in posterior contact with the rostral scales, five and four enlarged canthal scales on right and left sides of head, respectively; subdigital lamellae on phalanges II and III of fourth toe 26; femur length (taken as proposed by Ruibal and Williams, 1961) 22.4 mm; femur/snout-vent length ratio ($\times 100$) 31.1. Coloration in life: dorsal ground color black; head and nape olive with random black vermiculations; a narrow subocular yellowish semicircle; ventral ground color black, mottled with whitish; dewlap black centrally, edged with whitish; tail very dull gray-green to gray.

Variation

The series consists of 10 males (ranging from three adults with snout-vent lengths of 72 mm to a juvenile with a snout-vent length of 35 mm; males are easily distinguished because they possess a pair of enlarged postanal scales), and 13 females with snout-vent lengths of 61 mm to 29 mm. Scutellar variation may be summarized as follows (see also Table 1); I follow the schema used by Williams and Rand (1969).

Head.—Short, moderately broad posteriorly, the appearance being distinctly short-snouted. Head scales small to tiny, smooth to weakly striate in both sexes, smallest on occiput; 12 to 15 ($M_0 = 12$; mean = 12.4) scales across snout at level of second canthal scales; enlarged canthal scales three to six ($M_0 = 5/5$; the fractional designation used here and elsewhere denotes the counts on both sides of the head), the broad variation in this count being due to the relatively abrupt shortening of the most anterior canthal scales so that they become indistinguishable from adjacent snout-scales, counts ranging from 3/3 to 5/6 in the entire series. Nostril longitudinally oval; nasal scale in contact with rostral scale. Rostral scale short and low, about 2.5 times as wide as high, in contact with 4 to 8 ($M_0 = 6$; mean = 6.1) scales posteriorly (not counting nasal scales).

Supraorbital semicircles rather small, more or less parallel for the anterior halves, scales unicarinate laterally, the keels low in both sexes, separated by two to four ($M_0 = 3$) rows of small scales. A very distinct row of supraciliary scales, of which the anterior three are larger and almost shelflike, and more distinct than the much smaller posterior ones, the second (counting from the anterior) the most elongate. Posterior and mediad to the supraciliary row, about five irregular rows of small scales that blend almost imperceptibly into the enlarged scales of the supraocular disk, which has about six to 13 enlarged unicarinate scales, the gradation between the disk scales and surrounding scales making decisions as to what is an "enlarged scale" extremely difficult. Loreal rows five to seven ($M_0 = 5$; mean = 6.3), regularly arranged and generally rectangular or polygonal in shape. Temporal scales very tiny and granular, about 25 between the enlarged postocular scales and external auditory meatus. Interparietal scale not lying in a distinct depression in either sex, surrounded by 13 to 18 (mean = 15.8) small smooth scales. Interparietal very small, about one-third to one-quarter the size of the external auditory meatus; interparietal separated from supraorbital semicircles by six to 10 small scales (combinations include 6/6, 7/7, 7/8, 8/8, 9/9, 9/10, 7/9, 8/10; the first three categories with 5 individuals each). External auditory meatus relatively small, about 30 times as large as the largest bordering temporal scale, ventrally placed, and slightly above the level of the oral commissure.

Subocular scales always separated from supralabial scales by one row of scales, anteriorly grading into the loreal scales and posteriorly grading rapidly into the tiny temporals. Seven or eight supralabials to center of eye.

Mental scale large, semidivided, wider than deep, in contact with five to seven ($M_0 = 6$; mean = 5.9) postmental scales; one sublabial and one infralabial in contact with mental on each side. Throat scales elongate anteriorly, becoming increasingly smaller and circular to subcircular posteriorly.

Table 1.—Data for seven species of aquatic anoles. Characters given are: 1) largest male and female; 2) snout scales between second canthals; 3) vertical loreal rows; 4) scales between supraorbital semicircles; 5) scales between semicircles and interparietal; 6) scales around interparietal; 7) scales in supraorbital disk; 8) postrostrals; 9) postmentals; 10) dorsal scales in one head length; 11) ventral scales in one head length; 12) canthals; 13) fourth toe lamellae II + III; 14) scale rows between suboculars and supra-labials; 15) ratio femur length/snout-vent length.

Data on *A. barkeri* published by Meyer (1968) modify some data given here. The lowest interparietal scale count (character 6) and lowest femur/snout-vent length ratio in males (character 15) in *Anolis poeciloopus* are both from a specimen (MCZ 139348) that may be misidentified. The next-lowest value for scales around the interparietal is 17 (from KU 75964), and for femur length/snout-vent length ratio is 28.2 (KU 75966).

Charac- ter	<i>Anolis</i> <i>eugenegrahami</i> (N = 25)	<i>Anolis</i> <i>vermiculatus</i> (N = 15)	<i>Anolis</i> <i>barkeri</i> (N = 10)	<i>Anolis</i> <i>lionotus</i> (N = 28)	<i>Anolis</i> <i>aquaticus</i> (N = 19)	<i>Anolis</i> <i>poeciloopus</i> (N = 18)	<i>Anolis</i> <i>macrolepis</i> (N = 20)
1	$\delta = 72$, $\varphi = 61$	$\delta = 123$, $\varphi = 83$	$\delta = 95$, $\varphi = 78$	$\delta = 73$, $\varphi = 67$	$\delta = 73$, $\varphi = 63$	$\delta = 67$, $\varphi = 66$	$\delta = 62$, $\varphi = 55$
2	12-15 mean = 12.4 $M_0 = 12$	8-11 mean = 9.6 $M_0 = 9/10$	6-9 mean = 7.4 $M_0 = 8$	7-14 mean = 9.9 $M_0 = 9$	8-16 mean = 11.1 $M_0 = 10$	15-20 mean = 17.4 $M_0 = 16/18$	8-10 mean = 8.9 $M_0 = 9$
3	5-7 mean = 6.3 $M_0 = 6$	9-11 mean = 9.7 $M_0 = 9$	7-12 mean = 7.8 $M_0 = 8$	7-13 mean = 9.5 $M_0 = 9$	9-12 mean = 10.5 $M_0 = 10$	8-13 mean = 10.1 $M_0 = 9/11$	6-9 mean = 7.1 $M_0 = 6$
4	2 (9), 3 (13), 4 (1)	1 (1), 2 (12), 3 (2)	1 (8), 2 (2)	0 (5), 1 (10), 2 (12), 3 (1)	2 (3), 3 (7), 4 (9)	3 (5), 4 (13)	0 (10), 1 (10)
5	6/6 (5), 6/7 (5), 7/8 (5), 8/8 (4), 9/9 (1), 9/10 (1), 7/9 (1), 8/10 (1)	3/3 (1), 3/4 (1), 4/4 (6), 4/5 (3), 5/5 (2), 6/6 (1)	3/3 (1), 4/4 (5), 4/5 (2), 5/5 (1), 6/6 (1)	0/0 (1), 0/1 (1), 1/1 (12), 1/2 (8), 2/2 (5), 2/3 (1)	4/4 (1), 4/5 (1), 5/5 (1), 5/6 (2), 6/6 (1), 7/7 (5), 7/8 (1), 8/8 (1), 9/9 (2), 9/10 (1), 10/11 (1), 6/9 (1), 7/9 (1)	2/2 (1), 3/3 (2), 3/4 (1), 4/4 (4), 4/5 (2), 5/5 (2), 5/6 (1), 6/6 (2), 7/8 (1), 4/6 (1), 5/7 (1)	0/0 (5), 0/1 (4), 1/1 (11)
6	13-18 mean = 15.8	15-24 mean = 19.3	9-14 mean = 11.1	8-15 mean = 11.4	8-26 mean = 17.3	9-25 mean = 20.7	12-19 mean = 14.8

Table 1.—(Continued)

Char- acter	<i>Anolis</i> <i>eugeneagrahami</i> (N = 23)	<i>Anolis</i> <i>vermiculatus</i> (N = 15)	<i>Anolis</i> <i>barkeri</i> (N = 10)	<i>Anolis</i> <i>lionotus</i> (N = 28)	<i>Anolis</i> <i>aquaticus</i> (N = 19)	<i>Anolis</i> <i>poecilotropus</i> (N = 18)	<i>Anolis</i> <i>macrolepis</i> (N = 20)
7	6-13 mean = 8.3	7-16 mean = 11.3	6-12 mean = 8.7	2-10 mean = 5.1	10-23 mean = 16.1	7-15 mean = 11.1	3-6 mean = 4.4
8	4-8 mean = 6.1 M ₀ = 6	7-11 mean = 9.1 M ₀ = 9	3-10 mean = 7.1 M ₀ = 8	6-10 mean = 7.8 M ₀ = 8	8-11 mean = 9.3 M ₀ = 9/10	6-9 mean = 7.7 M ₀ = 8	6-9 mean = 8.1 M ₀ = 7
9	5-7 mean = 5.9 M ₀ = 6	4-8 mean = 5.9 M ₀ = 6	4-6 mean = 5.1 M ₀ = 6	5-10 mean = 7.1 M ₀ = 6	4-11 mean = 8.3 M ₀ = 10	6-8 mean = 6.7 M ₀ = 6	4-7 mean = 5.7 M ₀ = 6
10	40-56 mean = 46.0	50-63 mean = 55.8	36-43 mean = 39.8	21-38 mean = 29.5	33-52 mean = 40.8	30-49 mean = 39.7	19-27 mean = 22.1
11	37-63 mean = 49.5	45-61 mean = 52.6	33-52 mean = 45.0	33-55 mean = 41.3	30-44 mean = 36.1	34-52 mean = 41.3	28-45 mean = 37.6
12	3/3 (1), 4/4 (4), 4/5 (3), 5/5 (18), 5/6 (1), 4/6 (1)	4/5 (1), 5/5 (3), 5/6 (2), 6/6 (5), 6/7 (2), 7/7 (1)	4/4 (6), 4/5 (2), 5/5 (2)	3/4 (1), 4/4 (12), 4/5 (15), 5/5 (10)	3/3 (5), 3/4 (1), 4/4 (13)	3/3 (10), 4/4 (7), 5/6 (1)	3/3 (4), 3/4 (3), 4/4 (13)
13	23-29 mean = 25.9	27-31 mean = 29.1	15-18 mean = 16.5	15-18 mean = 16.0	12-17 mean = 15.3	13-19 mean = 16.6	13-17 mean = 15.4
14	1 (46)	1 (28), 2 (1)	0 (14), 1 (5)	0 (9), 1 (47)	1 (2), 2 (36)	0 (7), 1 (27)	0 (13), 1 (27)
15	♂: 30.1-32.2 mean = 31.1 ♀: 28.6-32.3 mean = 31.0	♂: 26.6-30.4 mean = 28.6 ♀: 27.8-31.1 mean = 29.3	♂: 26.3-28.7 mean = 28.2 ♀: 26.4-32.1 mean = 29.7	♂: 27.1-31.7 mean = 26.0 ♀: 26.5-31.1 mean = 28.5	♂: 27.8-31.8 mean = 30.0 ♀: 25.8-38.4 mean = 29.8	♂: 26.6-34.1 mean = 30.9 ♀: 27.1-32.0 mean = 30.3	♂: 29.0-34.5 mean = 31.6 ♀: 27.9-34.0 mean = 31.3

Trunk.—Dorsal scales small, a median zone of slightly larger scales, elongate rectangular and slightly keeled to smooth, 40 to 56 (mean = 46.0) in snout-anterior margin of ear distance, rapidly becoming smaller and granular on back and flanks, and somewhat larger (about four times) ventrally, the ventrals smooth and rounded, not overlapping; no middorsal crest scales; ventrals vaguely arranged in transverse rows, 37 to 63 (mean = 49.5) in snout-ear distance.

Dewlap.—Relatively small, absent in females, not inset or "slotted;" dewlap scales elongate to papillose, slightly larger than throat scales, slightly smaller than middorsal trunk scales; dewlap scales not arranged in well-spaced rows but rather crowded together, those along the free edge of the dewlap even more crowded and keeled; dewlap black to dark gray centrally, free edge whitish to very pale yellow.

Limbs and digits.—Limbs especially long, tibia length in adults about 1.3 times as great as snout-ear distance, hind foot about 1.2 times as long as tibia. Twenty-three to 29 subdigital lamellae under phalanges II and III of fourth toe. All enlarged limb scales uni- (on thigh and crus) or multicarinate (on pes), including supradigital scales. Anterior thigh scales much larger than granular posterior thigh scales and slightly larger than ventral scales.

Tail.—Very slightly compressed to a vertical oval in cross section, length in adults less than twice snout-vent length; middorsal caudal scales enlarged, almost spinose; tail strongly verticillate, with four or five middorsal scales per verticil and four or five unicarinate ventral scales per verticil near base of tail; lateral caudal scales unicarinate, about one-quarter size of ventral caudal scales; about four rows of enlarged ventral caudal scales; scales around base of tail and behind vent smooth and granular, comparable in size to lateral trunk scales.

Hemipenis.—Large, very weakly bilobed apically, the sulcate surface smooth, the nonsulcate surface with about four basal flounces and many small to tiny calyces apically.

Coloration and pattern.—*A. eugenegrahami* is weakly sexually dichromatic. The general appearance of both sexes in life is black or very dark gray. One male was noted as being greenish black. The dewlap in males is black with a white to very pale yellow edge, and there is in both sexes a pale yellowish subocular semicircle. In males, the venter is black to dark gray, mottled with whitish; tails are very dull gray-green to gray. Females are likewise black dorsally; laterally they are mottled with greenish, and there is a middorsal series of four ovate gray blotches (separated by black papilionaceous figures) that extends onto the yellowish green tail. In males, the head is olive green, in females grayish, with random black vermiculations. In females, the neck is olivaceous, and there is a hollow black-edged "collar." In females, the limbs are banded black to dark gray and olive to pale gray; the venter is pale olive to whitish.

Juveniles are like females, only more contrastingly colored; in addition there is a dull green flank stripe, with four black diagonal bars below it. There is a series of three black lines that extend onto the lower lip radiating from the eye and on a gray-green ground. Female (and assumably juvenile) patterns are more prominent during the day than at night, but in no way should these markings and pattern be considered bright. The general aspect of both sexes in life is of a very dark (black) lizard with a minimum of obvious pattern; juveniles are exceptional in that the flank stripe is moderately obvious even at night. The black female and juvenile "collar" is visible but not a striking feature; the same is true of the vermiculate head pattern.

Comparisons

The distinctive features of *A. eugenegrahami* distinguish it at once from all other known species of aquatic anoles. None is basically a black lizard. These species all have compressed tails, whereas the tail in *eugenegrahami* is very weakly compressed. *A. vermiculatus* lacks

a dewlap (and rather has a prominent transverse gular fold), whereas the dewlap colors in the remaining continental species are all bright (reds to oranges; dewlap color unknown in *A. macrolepis*), in contrast to the somber dewlap in *eugenegrahami*. The ventral scales are keeled in the other six species, small and virtually granular in *eugenegrahami*. Of these seven species, male *vermiculatus* are the largest (123 mm snout-vent length), *barkeri* ranks second (101 mm), and the remaining five species are about the same size (maximum sizes 62 to 76 mm in males).

Meristic data for the seven known aquatic species of *Anolis* are given in Table 1. I have made no effort to examine long series of those species other than *A. eugenegrahami*, and in one case (*A. barkeri*) published data expand the parameters of some scale counts. Nevertheless, the comparative data show the differences between the seven species and emphasize the differences between them and *A. eugenegrahami*. According to the Etheridge (1960) system, *A. vermiculatus* is an Alpha section anole and the remaining mainland species belong to the Beta section.

A. eugenegrahami has a mean of 12.4 snout scales between the second canthals; all other species with the exception of *A. poecilopus* (mean = 17.4) have lesser means (7.4 to 11.1). *A. eugenegrahami* has fewer loreal rows (mean = 6.3) than any other species (7.1 to 10.5). The modal number of scales between the supraorbital semicircles is one (*barkeri*), two (*vermiculatus*, *lionotus*), three (*eugenegrahami*), and four (*aquaticus*, *poecilopus*), with *macrolepis* evenly divided between zero and one. Scales between the interparietal and the supraorbital semicircles vary in *A. eugenegrahami* between 6/6 and 9/10 (modes 6/6, 7/7, 7/8—each with five individuals), in *A. vermiculatus* between 3/3 and 6/6 (mode 4/4), in *A. barkeri* between 3/3 and 6/6 (mode 4/4), in *A. lionotus* between 0/0 and 2/3 (mode 1/1), in *A. aquaticus* between 4/4 and 10/11 (mode 7/7), in *A. poecilopus* between 2/2 and 7/8 (mode 4/4), and in *A. macrolepis* between 0/0 and 1/1 (mode 1/1). The extreme variation in this character in *A. eugenegrahami*, *A. aquaticus*, and *A. poecilopus* is noteworthy. *A. eugenegrahami*, with a mean of 15.8, stands about midway in the series in number of scales around the interparietal (means of 11.1 in *A. barkeri*, 20.7 in *A. poecilopus*).

A. eugenegrahami has the lowest mean number (6.1) of postrostrals of the entire series; *A. barkeri* is next highest (7.1) and the highest is *A. aquaticus* (9.3); there is virtually no overlap in this count between *A. eugenegrahami* (four to eight) and *A. aquaticus* (eight to 11). As far as postmentals are concerned, *A. eugenegrahami* has a low mean (5.9), but those of *A. barkeri* (5.1) and *A. macrolepis* (5.7) are even lower; the high mean is that of *A. aquaticus* (8.3). The smallest dorsal scales are those of *A. vermiculatus* (mean = 55.8), the largest those

of *A. macrolepis* (mean = 22.1); *A. eugenegrahami* stands near the upper extreme (mean = 46.0). The smallest ventral scales are those of *A. vermiculatus* (mean = 52.6), the largest *A. aquaticus* (mean = 36.1); *A. eugenegrahami* stands near the upper extreme (mean = 49.5). Enlarged canthal scales in the entire series of species vary between 3/3 (*A. eugenegrahami*, *A. aquaticus*, and *A. poecilopus*) and 7/7 (*A. vermiculatus*). Modes are 3/3 (*A. poecilopus*), 4/4 (*A. barkeri*, *A. aquaticus*, *A. macrolepis*), 5/5 (*A. eugenegrahami*), and 6/6 (*A. vermiculatus*); *A. lionotus* has an anomalous mode of 4/5 (15 individuals), with incidences of 12 for 4/4 and 10 for 5/5. The two Antillean species, *A. eugenegrahami* and *A. vermiculatus*, have high fourth toe lamellae counts—23 to 29 in the former, 27 to 31 in the latter; these counts in the mainland species vary between 12 (*A. aquaticus*) and 19 (*A. poecilopus*). The scales between the subocular scales and the supralabials vary in the entire series from zero to two. A mode of zero occurs in *A. barkeri*, of one in *A. eugenegrahami*, *A. vermiculatus*, *A. lionotus*, *A. poecilopus*, and *A. macrolepis*, and of two in *A. aquaticus*. The highest mean femur length/snout-vent length ratio in each sex, all sizes combined, is that of *A. macrolepis* (males 31.6, females 31.3), with *A. eugenegrahami* second (males 31.1, females 31.0), and *A. lionotus* lowest (males 26.0, females 28.5). The extreme ratios in males vary between 26.3 (*A. barkeri*) and 34.5 (*A. macrolepis*), in females between 25.8 and 38.4 (both in *A. aquaticus*).

There is no need to compare *A. eugenegrahami* with any other Hispaniolan (or indeed Antillean) anole. Except for *A. vermiculatus*, none is aquatic; *A. eugenegrahami* is eminently distinct from that Cuban species. Both species are Alpha section *Anolis* according to the Etheridge (1960) schema, but *A. vermiculatus* belongs to a different series—the *lucius* series with four members, all of which are Cuban (see Williams, 1976b:14). No other Hispaniolan anole has a black dewlap with a white edge; although black is involved with the dewlap of *A. chlorocyanus*, the dewlap there is vertically bicolored, with the anterior portion pale blue and the posterior portion inky blue to black. The dewlap color, somber hues, and subdued pattern, as well as the habitat, all immediately distinguish *A. eugenegrahami* from all Antillean congeners. Pertinent comparisons with mainland aquatic species have been made above; once again, *A. eugenegrahami* is shown to be quite distinctive.

That *A. eugenegrahami* is unique from all other Hispaniolan anoles as well as from all other aquatic anoles is unquestioned. However, a troublesome fact remained; the species is so very different in such a variety of morphological (and ethological) characters that one is left without any obvious and certain Antillean relatives with which to associate it.

Ernest E. Williams was equally puzzled as to the affinities of *A. eugenegrahami*, and he, with the competent assistance of Susan Rhodin, made skeletal preparations of two of the MCZ paratypes. His amazement at the results is equal only to my own. *A. eugenegrahami* is an Alpha section anole (as expected) belonging to Etheridge's (1960) *bimaculatus* group, a group which on Hispaniola is otherwise represented only by the distichoid anoles (*A. distichus* Cope and *A. brevirostris* Bocourt and its allies). Williams (*in litt.*, 3 October 1977) stated that *A. eugenegrahami* is so assigned because it has "caudal vertebrae without transverse processes, lateral processes of the interclavicle divergent from the proximal parts of the clavicles, lower jaw smooth (i.e. without sculpturing present in some members of the *cristatellus* group). Splenial present. Pineal foramen at the fronto-parietal suture as a U-shaped notch on the parietal. Inscriptional rib formula 3:1 (3 attached, one free). The one feature in which *A. eugenegrahami* differs from Etheridge's 1960 description of the *bimaculatus* group is the size of the splenial. It is well developed as in *A. richardi*, . . . not small or absent as in previously known members of the group."

Williams's interpretation, following his own (1976b) excellent outline of the interrelationships of the Antillean anoles, is that he "would regard *eugenegrahami* as primitive on the basis of the large splenial . . . and would place it in the *bimaculatus* series as its own subseries and species group, placing it, as more primitive, ahead of the *stratulus* subseries, which includes the *evermanni*, *stratulus*, and *distichus* species groups. It may have been an early invader of Hispaniola from Puerto Rico, since the current hypothesis is that the *bimaculatus* series arose in Puerto Rico. The distichoids are undoubtedly late invaders of Hispaniola; this is to be inferred since they are a highly derived group originating from some pre-*stratulus* stock, and *stratulus* itself is highly derived."

I agree wholeheartedly with Williams' (*in litt.*) closing paragraph: "The discovery of this species is exciting beyond the ordinary. Not only is its ecology highly special but it is an apparent relict of a stock primitive for the *bimaculatus* series. It confirms our joint belief that the period of discovery and even of important biogeographic discovery is not yet ended in the West Indies." If I were to make one slight change in Williams's statement, it is that I would change "belief" to either "certainty" or "absolute conviction."

Remarks

I have already discussed in some detail the situation at the type-locality of *A. eugenegrahami*. The site is shown in Fig. 1. Some other observations are pertinent.

On our first nocturnal visit (4 August 1977; 2200 to 2400 h), we

encountered all specimens but one on rock faces. These were almost invariably dry faces; one individual was taken on a wet rock face (but not with water running over it). Most individuals were exposed on vertical rock faces, with a predilection for edges (where two vertical faces intersect to form a rather sharp edge). One individual was taken sleeping upside down in an open nook beneath a moderate-sized boulder. The exceptional lizard (a female) was taken 15 mm above the water, about 30 mm from the bank, on some hanging skimpy vegetation. All individuals slept soundly and were not easily disturbed either by talking or by light. One juvenile, when disturbed, leaped into a shallow (10 mm) pool and swam to the edge where it rested temporarily, and then "disappeared."

On the night of 5 August 1977, I secured a juvenile sleeping on a shrub, 15 mm above the boulder from which the shrub grew; other juveniles were taken sleeping head-up in vertical dry rock faces, and the single male was secured 1.2 m above the water on the edge of a vertical rock face. There seemed to be no effort made at concealment, because most lizards were in the open, and very obvious. Their dark coloration made them very conspicuous against the gray rocks. One large male is noteworthy in that he slept in an S-curve exposed but within a 10 by 20 mm flat cavity on the vertical rock face. Even this site was not an obvious attempt at concealment. The few lizards found on vegetation at night were likewise obvious, but I have the impression that this is not their normal sleeping site.

On Graham's and Thurmond's first diurnal visit, they noted the concentration of the "black" anoles on the rocks and mudbank at the base of the waterfall. They estimated that they saw 15 to 20 lizards, many of which were at the waterfall. Night collecting did not reveal any concentration (nor indeed any lizards) at this site; rather, the lizards were scattered between the waterfall and the old road culvert in a random manner—some widely spaced, others close together. We never secured two on the same boulder, unless a juvenile that sought refuge under my shirt and the sleeping male collected immediately thereafter were from the same huge boulder.

On 7 August 1977, Graham took photographs of the stream at 0945 h. While climbing the incline he saw a female run into a sandy-bottomed cranny 0.6 m above the water to seek refuge. Another female was 3 m from the water and 3.7 m high on a large rock. As noted previously, Graham and Thurmond both observed adults escaping under wet rocks and boulders and into rocky indentations behind the waterfall.

The type-locality is unique in this area. The new Ennery-to-Cap-Haïtien road leaves Ennery to ascend a major spur of the Massif du Nord, the Chaîne de Marmelade, which it crosses at Carrefour Mar-

melade (where a road goes to the east to the town of Marmelade) at 920 m, and then descends into the Plaisance valley (which lies at an elevation of about 305 m). From the town of Plaisance, the road ascends a low (280 m) minor spur of the Massif du Nord (the Morne Lafleur), and then descends to parallel the Rivière du Limbé in its valley to the town of Limbé, which is close to sea level. The type-locality lies on the northern slope of this Plaisance-Limbé montane spur. The elevation is not excessive (215 m), but the combination of a steep and boulder-strewn stream with remnant gallery forest is unique. In an attempt to find other localities for *A. eugenegrahami*, we night collected in an adjacent (but much smaller and narrower) stream without success. Two other streams at the same approximate elevation cross another road between Plaisance and Pilate, a few kilometers northwest of the former town. We visited both of these streams during the day; they are slow-moving and placid, due primarily, we assumed, to the fact that at that point in their courses they are in the flood plain of Les Trois Rivières and about to empty into that major stream.

The Plaisance valley is an enclosed, relatively high, valley; its southern and eastern margins are formed by the Massif du Nord itself, its western and northern margins by a series of small ranges (Morne Lafleur, Morne Crête Rouge, Morne Gris Mango), and finally, to the extreme east, the Morne Bonnet à l'Evêque, the latter merging to the south once more with the Chaîne de Marmelade. From the vantage of Carrefour Marmelade, one looks to the north and is impressed with the lushness of the Plaisance valley, its apparent enclosure, and the jumble of major and minor montane masses and massifs between the valley and the coast to the north and northwest. Although I feel certain that *A. eugenegrahami* is not limited to the Plaisance area (namely, in streams that drain the Morne Lafleur), other immediately adjacent regions have revealed nothing. The most likely area, the northern slopes of the Chaîne de Marmelade, lacks streams of any size and complexity; the few streams and rivulets where I collected in 1974 did not reveal *A. eugenegrahami*. One area suggests itself for further investigation, partially because it has the "right" sort of stream, but it is at a higher elevation. This is the area between Jonas and Dondon in the Morne Bonnet à l'Evêque. It is of course possible that *A. eugenegrahami* is widespread in these mountains and may even extend to the east as far as the northern slopes of the Cordillera Central in the República Dominicana. Too much of the northern slopes of the Massif du Nord is simply inaccessible today to make any generalizations about the range of this aquatic lizard.

I have one further comment. Every herpetologist or biological collector who has traveled from Port-au-Prince to Cap-Haïtien on the

north-south road has passed the type-locality of *A. eugenegrahami*. I myself did so many times in 1974. But the road has been in such terrible disrepair that one's attention was directed to it rather than to the surrounding countryside. In 1974, I was unaware of the beauty of this northern portion of Haiti; it is lush and mesic, despite the near absence of original forest cover (although some of that remains as shade trees in *caféières*). My whole impression of northern Haiti is now different, due primarily to the fact that one can now make this formerly arduous, and often hazardous, drive in a relaxed and observant state. That we stopped at Roche Parfait was chance; that Graham and Thurmond climbed the stream bed was due to their industry; that they observed a "black" anole there was a fluke. It is through such sequences of non-biological events that biological discoveries will continue to be made in the West Indies.

DISCUSSION

Antillean anoles come in two general "styles." Because the dewlap serves a dual function—that of territorial declaration and as a sexual recognition device between the two sexes of the same species—it is usually contrastingly and brightly colored in contradistinction to a less brightly colored or more drab body color and pattern (body colors are usually greens, tans, browns, and patterns are unicolor, lineate, spotted, or composed of chevrons or diamonds—the latter in females). This arrangement of a bright or contrasting dewlap and a relatively subdued body pattern is typical of most Antillean anoles. At the other extreme, the dewlap may be very reduced or absent; in such cases the body coloration and pattern are vivid, often gaudy, and complexly colored and patterned; the *hendersoni* group of Hispaniolan anoles is a prime example of this. *Anolis monticola* Shreve is another Hispaniolan example. Thus, to "compensate" for lack of, or reduced, dewlap, sexual recognition and territorial declaration at least must depend upon the distinctive and brightly colored body pattern.

A. eugenegrahami does not readily fall into either of these styles. The body colors are dull, somber, and dark; even the more clearly marked females are not to be construed as being vividly colored or patterned. Thus, one might reasonably expect that the male dewlap would be brightly colored, but such is not the case because the dewlap is black or dark gray with a white to pale yellow edge and is relatively small for the size of the lizard. It would thus seem that *A. eugenegrahami* contradicts what has been generally supposed to be a "rule" in body pattern-dewlap size and color correlation within anoles. It is intriguing also that the Cuban aquatic *A. vermiculatus* lacks a dewlap and has the body variegated with browns, bluish greens, and greens, once again not especially bright colors and with a random camouflage pattern.

One possible explanation may be that *A. eugenegrahami* occupies such a specialized niche that it has no competitors. Although we observed sleeping *A. cybotes* along the ravine (always on shrubs adjacent to the water, never on rocks), I feel sure that *A. distichus* and *A. chlorocyanus* are likewise present, along with the giant *A. ricordi* Duméril and Bibron in the crowns of the trees. Of these four species, *A. ricordi* is much larger in snout-vent length (males to 160 mm), rarely comes to the ground, and surely never sleeps on rocks or carries on its diurnal activities immediately associated with streams and their beds. It is a brightly colored (green) lizard with a large peach colored dewlap. *A. distichus* is also an arboreal anole; it does, however, venture close to the ground on tree trunks and shrubs and may even be seen on ground litter and rocks. It is mottled greenish, small (local subspecies snout-vent length 58 mm in males), with a pale yellowish to yellowish with an orange central blush dewlap. *A. cybotes* is a stocky tree- and shrub-dwelling anole, but it is not averse to foraging or sunning on rock and cliff faces. The dewlap is very pale yellow to white in northern Haiti. *A. chlorocyanus* is vivid green and long-snouted with a relatively small bicolor dewlap; adult males are slightly smaller in snout-vent length than *A. eugenegrahami*. It is an arboreal anole, seldom coming to the ground to forage. Although it may occur on low shrubs, I have never seen it in strictly terrestrial situations. Thus, the two species with which *A. eugenegrahami* might be most closely associated ecologically and behaviorly are *A. cybotes* and *A. distichus*. The former is much stockier, has a large pale dewlap, and has a pale tan to reddish tan ground color with a greenish lateral stripe. *A. distichus* is smaller, mottled green in color, and has a moderate sized pale dewlap. It would be very difficult indeed for either of this duo of anoles to become confused, if and when they come in contact directly either as far as territory or sex is concerned, with *A. eugenegrahami*, or vice versa. The latter species bears little total resemblance to either *A. cybotes* or *A. distichus* in size, body shape, or habits.

There remain, then, the drab coloration and small dewlaps of *A. eugenegrahami*. The former may possibly be explained as an ecological-camouflage effect—inhabiting well-shaded ravines without any other close competitors, *A. eugenegrahami* may well have evolved a drab pattern to conform to the darkness of its habitat. It does not need to be brightly or contrastingly colored to declare its identity, because no other anoles are likely to occur precisely syntopically with it. The small and black dewlap may be interpreted similarly, that is, in shaded and dull ravines, without competitors, an elaborate and bright dewlap is unnecessary. The most likely candidate that a male *A. eugenegrahami* will encounter for mating is a female *A. eugenegrahami*—this is the only species with such specialized habitat and ecological requirements. If the dewlap is used for territorial declaration in this species

(and there is a possibility that it is not), its display may well be correlated with posturing that enhances the effect of the somber coloration and small dewlap. In the gloom of such a shaded ravine, the pale dewlap *edge* might be more striking than the dark dewlap itself. The comments of Williams and Rand (1977) on multiple-anole faunas are indeed pertinent in the context of *A. eugenegrahami*.

Richard Thomas has pointed out to me that the primitive anoline *Chamaelinorops barbouri* Schmidt, which is also Hispaniolan, has a similarly patterned dewlap; in this case the dewlap is basally dark brownish black with a whitish-to-cream colored edge. *C. barbouri* is a mesic forest anoline and typically is encountered in very shaded situations. The similarity of dewlap pattern (but not particularly coloration) may well be a response to the dull and shaded situation in which both it and *A. eugenegrahami* exist. The body color of *C. barbouri* is basically dark brown, at times with a greenish tinge. Thus, both body and basal dewlap are difficult to distinguish in the gloom of mesic forests; this would seem to make the brighter dewlap edge all the more contrasting and conspicuous when the dewlap is erected.

It would be exceptionally neat if we could state that the dark coloration of both sexes of *A. eugenegrahami* helps in their nocturnal camouflage while they sleep on boulders. At least at this site, this is not the case because the dark colors contrast sharply with the pale gray rocks; the female pattern, dark at night, is not disruptive. Only the juveniles, with an even more complex pattern than females, are slightly difficult to detect, but they, too, are conspicuous. The dark hues of *A. eugenegrahami* must function best during their diurnal activities.

ACKNOWLEDGMENTS

My primary debt of gratitude is to Eugene D. Graham, Jr., and Thomas M. Thurmond for their competent assistance in the field. I have borrowed comparative material from the following institutions and am grateful to the respective curators for these loans: American Museum of Natural History (AMNH), Richard G. Zweifel and George W. Foley; Museum of Natural History, The University of Kansas (KU), William E. Duellman; Museum of Comparative Zoology, Harvard University (MCZ), Ernest E. Williams; Museum of Zoology, The University of Michigan (UMMZ), Arnold G. Kluge. Jay Cole, Howard W. Campbell, William E. Duellman, and Ernest E. Williams have given freely of information at their disposal or helped with literature. Dr. Williams has most generously offered information from his great store of knowledge on anoles in general, and in this case especially those of the continental mainland. Specimens of *A. vermiculatus*, collected by me and now in the AMNH, were taken under National Science Foundation grants G-3865 and G-6252.

SPECIMENS EXAMINED

Anolis vermiculatus.—CUBA. Pinar del Río: San Vicente (AMNH 81302—2 specimens; AMNH 81303—4 specimens; AMNH 82304; AMNH 81305—6 specimens); 13.6 km W San Vicente (AMNH 82306); north base, Pan de Azúcar (AMNH 81307).

Anolis barkeri.—MÉXICO. Oaxaca: Cerro Azul, La Gloria (MCZ 58221). Veracruz,

Río Basura, 4.0 km NW Sontecomapán, Los Tuxtlas (MCZ 92103); between Laguna Catemaco and Volcán Santa Marta (UMMZ 121177–83). *Chiapas*, 4.8 km S Soluschiapa (MCZ 85008).

Anolis lionotus.—COSTA RICA. *Alajuela*: Cinchona, 488 m (MCZ 92955–64). *Limón*: Madre de Dios (MCZ 129351–54). PANAMÁ. *Colón*: El Valle, 560 m (KU 75952–58). *Coclé*: Achiote, 40 m (KU 75951). *Panamá*: Cerro Campana (KU 127713–14); south slope, Cerro Campana (KU 75948–50).

Anolis aquaticus.—COSTA RICA. *San José*: 15 km SW San Isidro El General, 865 m (MCZ 92902). *Puntarenas*: ca. 1.6 km SE Golfito (MCZ 92901); Rincón de Osa (MCZ 96553, MCZ 110412, MCZ 110571–72, MCZ 109967–69). PANAMÁ. *Chiriquí*: 16 km NE El Volcán, 1,170 m, (KU 107944–49); 9 km NW El Volcán, 1,170 m (KU 107950–52); Finca Ojos de Agua, southeast slope Cerro la Pelota, 1,440 m (KU 107953).

Anolis poecilopus.—PANAMÁ. *Colón*: 3.5 km SE Puerto Pílon, 230 m (KU 113256). *Panamá*: southeast slope, Cerro Jefe, 660–700 m (KU 113251–55, KU 94650). *Canal Zone*: stream near lodge on Pipe Line Road (MCZ 139348). *Darién*: Laguna, 820 m (KU 75962); Tacarcuna, 550 m (KU 75963–69); Quebrada de Taqua, 510 m (KU 75970–71).

Anolis macrolepis.—COLOMBIA. *Chocó*: Río San Juan, Caño Docordo between Currupí and Noanama (MCZ 112317–35). *Condoto*: Peña Lisa, 92 m (MCZ 70224).

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ARTICLE 12

STYLISTIC ANALYSIS OF STONE PENDANTS FROM LAS HUACAS BURIAL GROUND, NORTHWESTERN COSTA RICA

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ABSTRACT

An analysis of stone pendants and maces from the Las Huacas burial ground resulted in the identification of three distinct iconographical bird groups—harpy eagles, three-dimensional quetzals, and two-dimensional quetzals. A stylistic analysis of the stone pendants from each group using scalogram techniques revealed a clear artistic sequence for Las Huacas stonework. An approximate chronology for this sequence was established through the analysis of Las Huacas pottery. Results of the study suggest the local development of this art style.

INTRODUCTION

Although a large amount of Costa Rican jade work and other stonework is contained in private collections and museums, relatively little has been obtained through formal archaeological excavation. As a result, no clear chronology for this stonework presently exists, and little analysis other than basic description and classification has been attempted (Lothrop, 1955; Easby, 1968). The present work is an analysis of the richest available collection of Costa Rican stonework, in the context of associated artifacts and field records, which presently exists. The collection has been iconographically identified, classified and

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Fig. 1.—Map of Costa Rica showing the location of the Las Huacas site.

stylistically analyzed. An approximate chronology of stylistic types, to which other examples of this type of Costa Rican stonework may be compared, has been established through the analysis of Las Huacas pottery.

SITE AND COLLECTIONS

In 1903, Carl V. Hartman, then curator of the Archaeology and Ethnology Section of the Carnegie Museum of Natural History, obtained a collection of archaeological material from the Las Huacas burial ground site in the Nicoya Peninsula of northwestern Costa Rica. The location of the site, which Hartman described as being, "About four leagues southeast of the pueblo of Nicoya . . . (near a) . . . mountain pass named La Quebrada de las Guacas" (Hartman, 1907:12) is indicated on Fig. 1. Hartman purchased two large

Table 1.—*Frequencies of pottery types from the Las Huacas subcollection.*

Period	N	%
Zoned Bichrome	22	18.0
Zoned Bichrome-Linear Decorated	52	42.6
Linear Decorated	40	32.8
Early Polychrome	8	6.6
Total	122	100

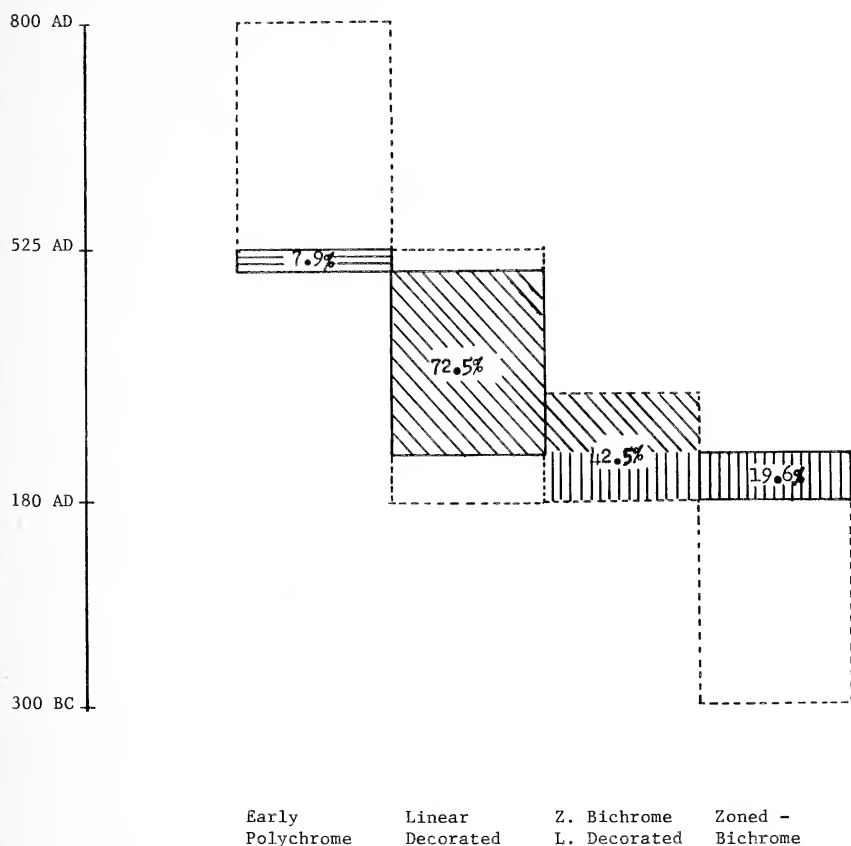


Fig. 2.—Ceramic chronology of the Las Huacas site.

collections from the Father Jose Maria Velasco (designated Velasco I and Velasco II), an amateur archaeologist from whom Hartman received permission to further excavate the site. Hartman's more scientifically obtained collection is designated Las Huacas. The Las Huacas burial ground collection thus consists of three subcollections, which together comprise the objects of this study. The collection contains both utilitarian objects and jewelry, the latter consisting of 1535 pendants, 464 beads, 63 maces, and 17 earrings.

Efforts to formulate an absolute chronology for the Las Huacas site are limited by the lack of available material that can be dated using radiometric techniques or other appropriate methods. An approximate chronology, however, can be established by utilizing the pottery typology sequence established for the area by Baudez and Coe (1962) and later refined by Baudez (1967). Because only the Las Huacas subcollection was systematically excavated, pottery from this subcollection alone was used for primary analysis. The subcollection contains pottery types from the Zoned Bichrome, Linear Decorated, and Early Polychrome periods (Baudez, 1967). Thirteen middle and late

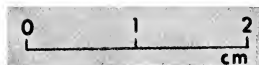
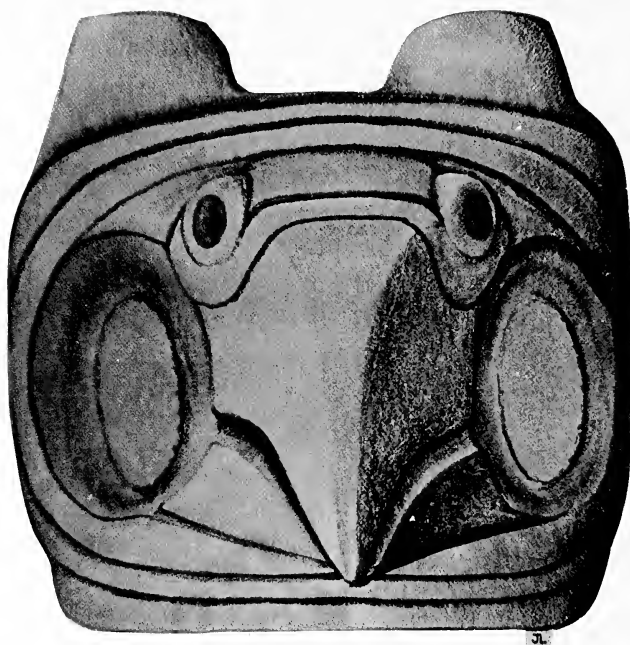


Fig. 3.—Harpy eagle representation on a stone club head illustrating the diagnostic harpy eagle features.

polychrome potsherds in the Las Huacas subcollection were considered to be a contamination by subsequent human activity at the site and were not used in the following analysis. The majority of pottery consists of Zoned Bichrome and Linear Decorated types. Frequencies are summarized in Table 1.

The Velasco I and Velasco II subcollections exhibit similar distributions with the exception of a large quantity of Middle and Late Polychrome vessels in the Velasco II subcollection. Hartman suggests that this was due to Velasco's method of collection: "An extensive collection of pottery . . . (was) gathered from various localities in the neighborhood of the pueblo of Nicoya" (Hartman, 1907:14).

The resulting chronological sequence of the burial ground is illustrated in Fig. 2 in accordance with the pottery percentages for the periods. In developing this chronology, only the unique ceramic characteristics of each period have been used, although pottery types serving as indicators of cultural continuity often overlap two periods. The Las Huacas site may therefore be placed at about A.D. 180 to A.D. 525 with a duration of approximately 345 years.



Fig. 3.—Continued

While the stonework consists of numerous iconographical representations, including humans, anthropomorphic birds, bats, amphibians, turtles, and felines, it was decided to confine quantitative analysis to two relatively populous, well-defined, and well-characterized iconographical bird groups—the harpy eagle (*Harpia harpyja*) and the quetzal (*Pharomachrus mocinno*).

The harpy eagle has been identified primarily by its characteristic features of facial disc, tuft, and beak. The feathers of the head tend to rise on an excited harpy eagle, resulting in a distinctive pattern in which two feather groups over the head resemble horns and in which facial feathers simulate lines along the face. In addition to these characteristics, the harpy eagle has the massive and powerful beak typical of a bird of prey, with visible nostrils over a cere area. The bird is not uncommon in the area of Las Huacas; Slud (1964:66) reports that, "the species is probably widespread in forest regions along both slopes from the lowlands into the upper middle altitudes." Twelve club heads and 103 pendants are harpy eagle representations. Only the pendants (herein designated as the Harpy Eagle population) were sufficiently numerous for seriation analysis. Fig. 3 illustrates a harpy eagle representation displaying the above described features.

The quetzal has been identified by its characteristic features of tuft, tail coverts, and posture. The tuft of this particular species runs horizontally over the head, a distinctive feature in Costa Rica. The tail coverts, longer than the body, and the erect posture with protruding breast further identify the bird as the species iconographically represented. Of the three subspecies of quetzals, *P. m. costaricensis* seems most likely to be represented by the stonework primarily because of its geographical distribution (Peters, 1945:148; Slud, 1964:164). Fig. 4 illustrates two quetzal representations. Seventy five pendants are quetzal representations, of which 45 are two-dimensional (designated Quetzal A population) and 30 are three-dimensional (designated Quetzal B population).

Despite the frequent emphasis on jade in the description and analysis of Costa Rican

Table 2.—Frequencies of mineral materials in Las Huacas iconographical bird group stonework.

Mineral	Harpy Eagles		Quetzal A		Quetzal B		Total	
	N	%	N	%	N	%	N	%
Feldspar	44	42.72	8	17.78	13	43.33	65	36.52
Serpentine	18	17.48	8	17.78	3	10.00	29	16.29
Jade	16	15.53	7	15.55	1	3.33	24	13.48
Antigorite (serpentine)	5	4.85	5	11.11	5	16.67	15	8.43
Prehnite	5	4.85	7	15.55	2	6.67	14	7.87
Diopside	4	3.88	—	—	6	20.0	10	5.62
Metadiorite	4	3.88	2	4.45	—	—	6	3.37
Jasper	2	1.95	3	6.67	—	—	5	2.81
Steatite	1	0.97	—	—	—	—	1	0.56
Zoisite	1	0.97	—	—	—	—	1	0.56
Actinolite	1	0.97	—	—	—	—	1	0.56
Unclassified	2	1.95	5	11.11	—	—	7	3.93
Total	103	100	45	100	30	100	178	100

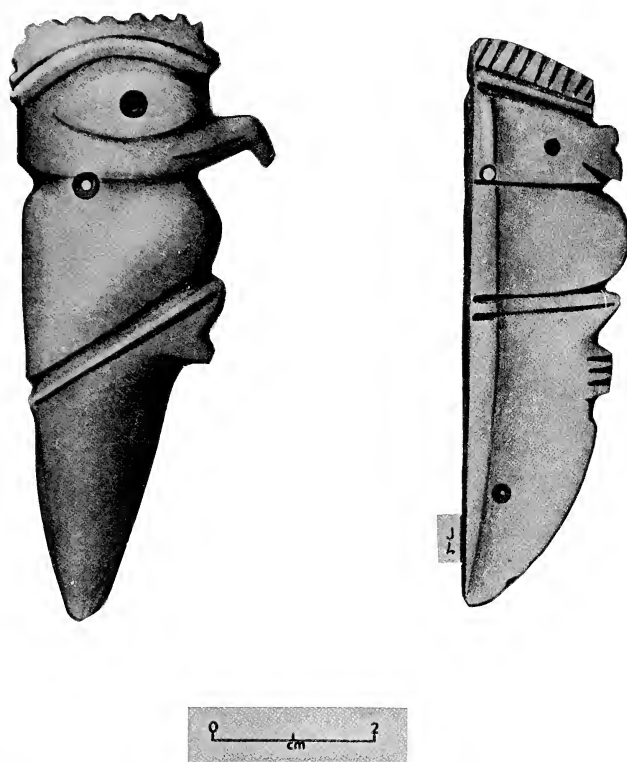


Fig. 4.—Quetzal representation on a stone pendant illustrating the diagnostic quetzal features.

stonework, only about 13% of the artifacts in the three populations were jade. The most common material was feldspar (37% of the artifacts) followed by serpentine (17%). Table 2 lists frequencies of the various materials used.

An incompletely worked jade pebble suggests that raw materials were obtained as smooth pebbles from stream beds (see Fig. 5).

STYLISTIC SERIATION ANALYSIS

Working under the assumption that within the same cultural tradition, cultural change will be gradual (Willey and Sabloff, 1974:99), we have attempted a classification and ordination of artifacts on the basis of stylistic change. As Deetz (1967:32–33) suggests, “If one is familiar with his material . . . (it is possible to) perceive certain relationships in the decorative style, shape, and proportions, which can be ordered in such a way as to produce a chronological sequence . . . since there



Fig. 5.—Incompletely worked jade pebble approximately 11.7 by 5.9 by 4.3 cm.

is a certain logical way to arrange the designs to achieve the most economical arrangement based on style change." We have employed Guttman scale analysis as a means for arriving at a stylistically-based ordination of artifacts.

Guttman scaling is a particularly powerful technique for ordering data which is the expression of a single underlying variable, such as time. Carneiro (1962) and Carneiro and Tobias (1963) have used Guttman scales for diachronic analysis in their investigation of cultural evolution. Wicke (1971) has used simple scalograms in his analysis of the Olmec art style. The technique used here builds upon Wicke's methodology by analyzing a fairly large and complex population of artifacts, by utilizing interactive computer analysis to build scalograms, and by employing certain mathematical indices to assess the reliability of resultant scales.

The first step in such an analysis is to separate the artistic features



Fig. 6.—Harpy eagle pendants illustrating various stylistic units.

of each set of figures into their diagnostic parts such that each part is a discernable stylistic unit (Roe, 1974:10). For the Harpy Eagle population, the following stylistic units were isolated: tuft; facial design; eyes; legs; beak; wings. Each pendant was coded for the presence or absence of each stylistic feature, with the exception of beak and wings for which elaboration or lack of elaboration was coded. Elaborate beaks were considered to be those in which nostrils are represented and where the remainder of the beak is either distinctive in relief or separated into inferior and superior mandibles. Elaborate wings are differentiated from the rest of the features by volume and/or contain incised feather representations. Variation in the above stylistic units is illustrated in Fig. 6.

The stylistic features of the Quetzal A population were legs, eyes, and breast (present or absent) and tuft, beak, and tail (elaborate or less elaborate). Elaborate tufts have been separated from the head by incised lines and/or have incised feather representations. Elaborate beaks have differentiated superior and inferior mandibles, whereas elaborate tails have been differentiated from the remainder of body by their particular shape and/or have feather representations.

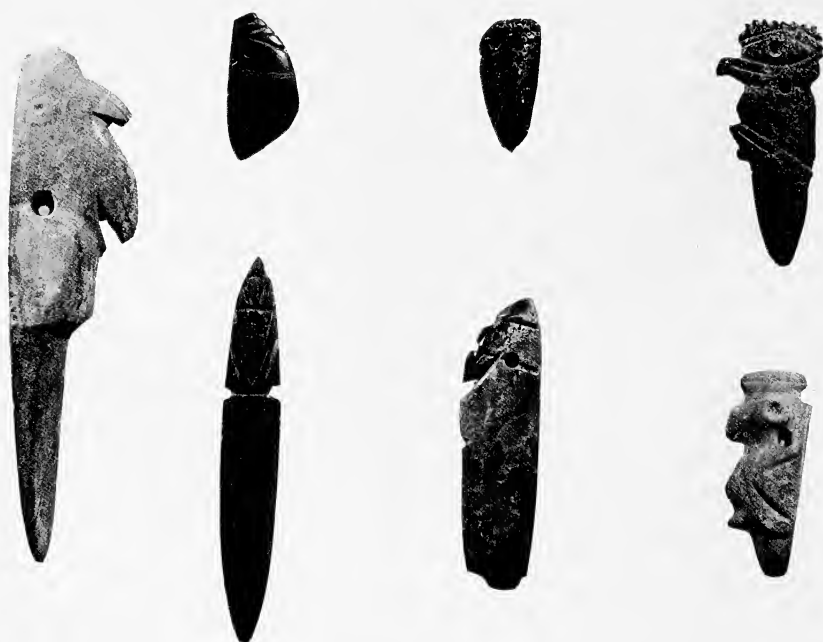


Fig. 7.—Quetzal pendants illustrating various stylistic units.

Stylistic features of the Quetzal B population were legs, eyes, breast, and wings (present or absent) and beak, tail and tuft (elaborate or less elaborate). Elaborate beaks have nostrils and are differentiated from the body by their volume or have superior and inferior mandibles represented. Elaborate tails are separated from the body either by a specific shape or by incised or grooved lines. Elaborate tufts are well differentiated from the remainder of the head and have one or more incised lines simulating feathers. Variation in the stylistic units of the quetzal populations are illustrated in Fig. 7.

We attempted to scale certain metric data together with the stylistic units described above, but in all cases the measurements and indices proved to be too capricious for meaningful unidimensional scaling. It appears that the size of the available material dictated to a great extent the dimensions of the object, an observation in keeping with our hypothesis concerning the provenience of materials as pebbles from stream beds. There do not appear to be any differences in sizes or proportions of objects through time.

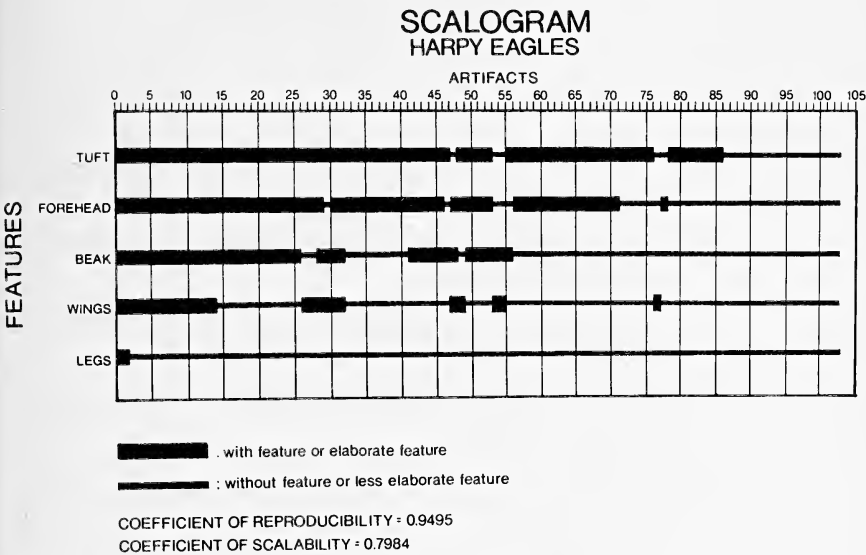


Fig. 8.—Scalogram for harpy eagle pendants illustrating stylistic change.

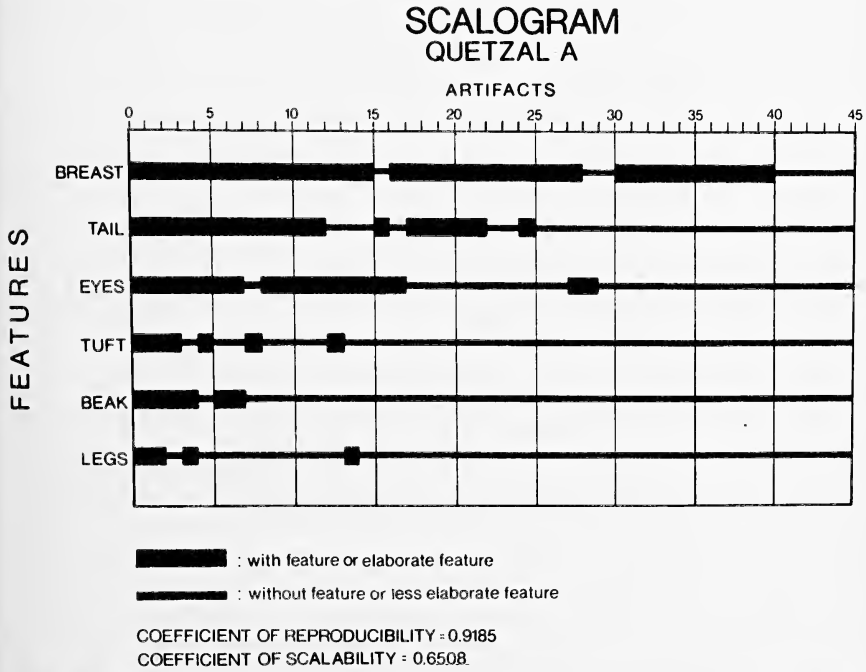


Fig. 9.—Scalogram for two-dimensional quetzal pendants illustrating stylistic change.

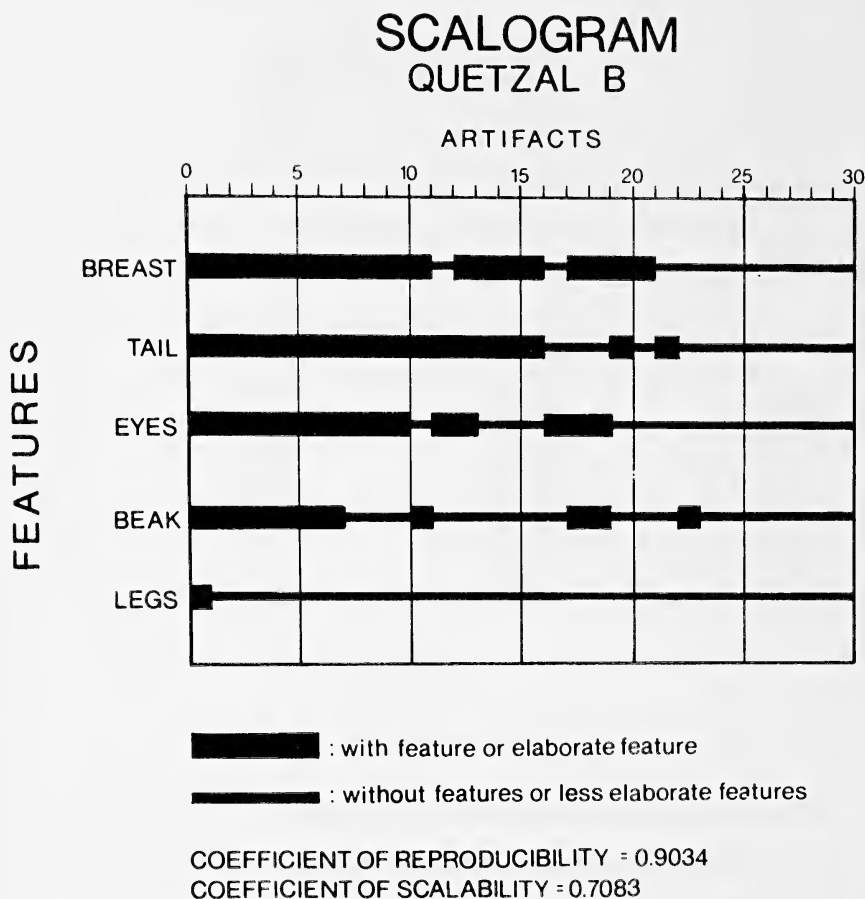


Fig. 10.—Scalogram for three-dimensional quetzal pendants illustrating stylistic change.

Scale Construction and Evaluation

Given the above universe of attributes for each subsample, three scalograms were constructed using the SPSS GUTTMAN SCALE subprogram (Nie et al., 1975). For the Harpy Eagle population, the eye feature did not seem to be part of the unidimensional relationship displayed among the other features and was consequently eliminated from further analysis. Similarly, the wing and tuft features were not used in the construction of the Quetzal B scale. All three scalograms show a high unidimensional and cumulative relationship among the features, indicating a single underlying variable which we postulate to be time. Scalograms are graphically illustrated in Figs. 8, 9, and 10.

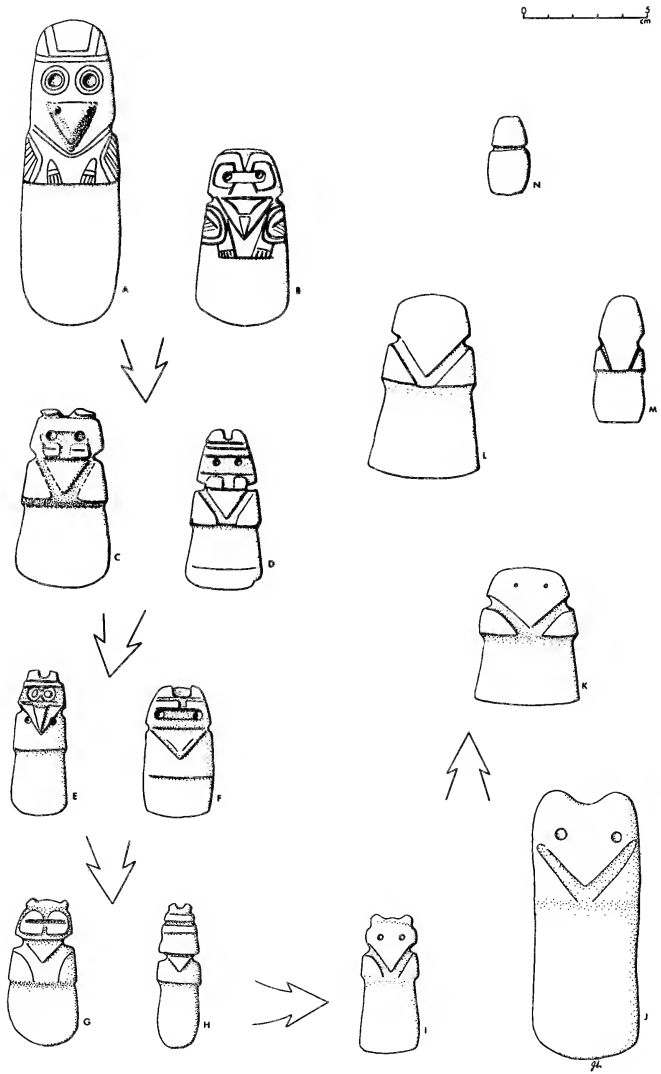


Fig. 11.—Diagram illustrating stylistic change in the harpy eagle pendants in accordance with Guttman scale analysis.

The scalograms have been evaluated by the coefficient of reproducibility, a measure of the extent to which an artifact's scale score is a predictor of its artistic pattern (or, more crudely, a measure of the number of errors in the scale) and the coefficient of scalability, an index of the extent to which the observed relationship is truly unidi-

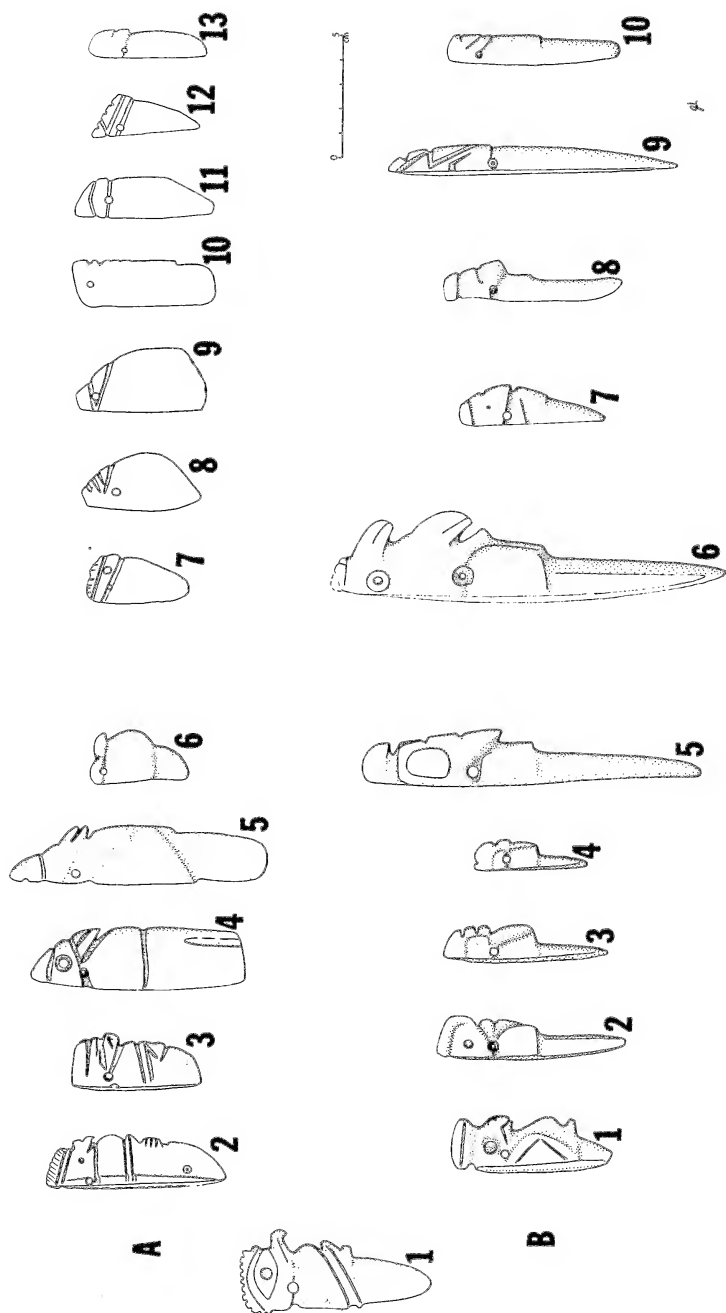


Fig. 12.—Diagram illustrating stylistic change in quetzal pendants.

Table 3.—*Ordering of stylistic changes indicating elaboration of features (+) versus absence or lack of elaboration (-).*

Harpy Eagle Pendant Group				
Legs	Wings	Beak	Facial Design	Tuft
+	+	+	+	+
-	+	+	+	+
-	-	+	+	+
-	-	-	+	+
-	-	-	-	+
-	-	-	-	-

Quetzal A Pendant Group					
Legs	Tuft	Beak	Eyes	Tail	Breast
+	+	+	+	+	+
-	+	+	+	+	+
-	-	+	+	+	+
-	-	-	+	+	+
-	-	-	-	+	+
-	-	-	-	-	+
-	-	-	-	-	-

Quetzal B Pendant Group				
Legs	Beak	Eyes	Tail	Breast
+	+	+	+	+
-	+	+	+	+
-	-	+	+	+
-	-	-	+	+
-	-	-	-	+
-	-	-	-	-

dimensional and cumulative. Both coefficients vary between 0 and 1, with 1 representing the perfect scale. A scale with coefficient of reproducibility above .9 and coefficient of scalability above .6 is generally accepted to be valid (Nie et al., 1975:533). The best scale was obtained for the populous Harpy Eagle pendant group, but all three scales were within acceptable limits.

We thus conclude that there was, in fact, gradual and orderly diachronic development of an art style in this area of northwestern Costa Rica. The Guttman scales indicated the major changes in the population through time, and chronologically ordered the artifacts. Table 3 indicates the ordering of the major stylistic changes in a perfect Guttman scale.

Direction of Change

Although Table 3 indicates relative chronology of artifact types, no direction of change is indicated. The artistic tradition may be devel-

































































































































































































































































LEGS	WINGS	BEAK	EYES	FACIAL DESIGN	TUFT
6		 	 		 
5	  	    	    	    	    
4	    	         	         	         	         
3	    	         	         	         	         
2	    	         	         	         	         
1	    	         	         	         	         
0	    	         	         	         	         

Fig. 13.—Progressive change in stylistic units of the harpy eagle pendants in accordance with Guttman scale analysis. The “eyes” unit has been included for comparison with other stylistic units.

oping from less elaborate to more elaborate representation or vice versa. We hypothesize that change was in the direction of realistic to stylized based on stratigraphic evidence.

Two levels have been established for Las Huacas burials—1.0 to 1.75 m (8 graves) and 1.75 to 2.25 m (11 graves). In the first level, three graves (Hartman, 1907:18, 23, 25; Plate XLVII; graves VIII, XIII, XIVb) have pottery of the Linear Decorated period. From the second interval, grave IX (Hartman 1907; Plate XLVII) has pottery from the Zoned Bichrome period together with an elaborate pendant (Hartman, 1907:Fig. 15). The relative depth from which the pendant was excavated, together with its association with pottery of an earlier type indicate the early existence of complex pendants. This hypothesis is further supported by a simple harpy eagle pendant found in the eastern corner of the burial ground. The pendant was not associated with a burial, but Hartman lists its profundity as only 0.9 cm suggesting a later origin for this artifact (Hartman, 1907:Fig. 51).

Figs. 11 and 12 illustrate the hypothesized direction and degree of change through time. Fig. 13 is a detailed representation of increasing simplification of features in the Harpy Eagle population through time.

CONCLUSIONS

The Guttman scale analysis suggests a gradual change in art style through time rather than the simultaneous existence of distinct styles. By assuming a constant rate of change, an approximate date for any stone pendant can be arrived at by dividing the 345 year duration of the Las Huacas site into equal periods corresponding to the number of major stylistic changes for the particular iconographical representation and matching the artifact with its associated period. Although the resulting date would be at best only a rough approximation, and although we are not certain that the direction of change is in fact towards increasing stylization, the method gives a better approximation than was previously possible for northwest Costa Rican stonework of this type. An additional contribution of the study was the identification of the actual bird species represented in the stonework, enabling the use of morphological characteristics for the quantitative analysis of artistic features.

The existence of a clear sequence of artifact types, illustrated in Figs. 11, 12, and 13, indicates a gradual stylistic development in northwest Costa Rica, and suggests the local manufacture of the artifacts. Some objects of the groups herein designated as Quetzal B have been reported from the other side of Costa Rica, in the Atlantic coastal area (Baudez, 1967:Plate 154), as have Harpy Eagle representations (Stone and Balser, 1965:Fig. 3d). Because the artifacts found in the Atlantic area do not appear to be part of a local artistic tradition, possible trade

contacts between the Atlantic and northwest Pacific Costa Rican areas are thus indicated by these data.

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SOUTH AMERICAN AND MAYAN CULTURAL CONTACTS AT THE LAS HUACAS SITE, COSTA RICA

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ABSTRACT

This study deals with two llama effigies, nine mirror backs, a bead, face pendant, and a reptile effigy from the Las Huacas site in Costa Rica. These artifacts are discussed and described and it is concluded that they reflect prehistoric cultural contacts with both the Central Andes and the Mayan region.

INTRODUCTION

The recent analysis of the Hartman collection in the Carnegie Museum of Natural History has revealed artifacts from Costa Rica that reflect cultural contacts with the Maya region and South America. The Carnegie collection was made by Carl V. Hartman (1907) in 1903 by excavation and through purchase. This collection is comprised of thirteen subcollections, secured from different areas of Costa Rica (Tables 1 and 2). The three collections pertinent to this discussion are the two collections purchased from Father Jose Maria Velasco and Hartman's excavations at the Las Huacas cemetery, located on the Nicoya Peninsula (Fig. 1).

The excavated ceramics from Las Huacas include early polychromes, zones bichromes, and linear decorated wares. On the basis of the chronologies established by Baudez and Coe (1962; Baudez,

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Fig. 1.—Map of Costa Rica showing location of Las Huacas site.

1967) and the percentage of each type in the collection, the cemetery can be dated to between 180–525 A.D. The stone pendants from Las Huacas have been seriated and also demonstrate that the cemetery was utilized for at least a 300-year period (Fonseca and Scaglion, 1978).

CAMILIDAE ARTIFACTS FROM LAS HUACAS

Two stone heads of what we have interpreted as representing members of the Camilidae were found in the Velasco 1 collection from the Las Huacas cemetery. The two heads were described by Hartman (1907: Plate 39—14, 22). The first (catalog no. 2939-1273, Figs. 2a, 3b, 4a, 5a–b) is the complete steatite head of a camelid measuring 3.1 cm in length, 1.9 cm in width, and 1.8 cm in thickness. A biconically drilled hole is situated at the position of the ear opening. The eyes have been partially drilled by the same technique. The skull has its maximum width over the eyes and the cheekbones stand out, in contrast to the depressed jaw lines. The nose and mouth are predominantly outlined by incised lines and the ears are laid back at the sides of the skull (see Figs. 7a and b for comparisons).

The second head (catalog no. 2939-1272) is made of serpentine and is another probable camelid, broken at the neck (Figs. 2b, 3a, 4b, 6a–b). This piece appears to be the head of a full bodied figure. Its ears

Table 1.—*Subcollections from North Pacific area: Nicoya Peninsula, Costa Rica.*

Name of subcollection	Method of acquisition	Date	Obtained by	Provenance	No. objects in catalog
Las Huacas	Fieldwork	1903	Hartman	Archaeological Site: Las Huacas	481
Chira	Fieldwork	1903	Hartman	Chira Island Shells-heaps	23
Velasco No. I	Purchase	1903	Hartman from Velasco	Archaeological Site: Las Huacas	3,851
Velasco No. II	Purchase	1903	Hartman from Velasco	Mostly archaeological site: Las Huacas	2,181
Ferraz No. I	Purchase	1903	Hartman from Ferraz	Other part: Nicoya neighborhood Near Nicoya	29
Total					6,565

Table 2.—*Subcollections from Central Plateau and Atlantic area, Costa Rica.*

Name of subcollection	Method of acquisition	Date	Obtained by	Provenance	No. objects in catalog
Ferraz No. II	Purchase	1903	Hartman from Ferraz	Central Plateau	538
Troyo	Purchase	1903	Hartman from Troyo	Central Plateau	3,197
Concepcion	Fieldwork	1903	C. V. Hartman	Central Plateau	341
Curridabat	Fieldwork	1903	C. V. Hartman	Central Plateau	779
San Miguel	Fieldwork	1903	C. V. Hartman	Central Plateau	32
Las Mercedes	Fieldwork	1903	C. V. Hartman	Atlantic Area	26
Irazu	Fieldwork	1903	C. V. Hartman	Central Plateau near Irazu Volcano	3
Chinchilla	Fieldwork	1903	C. V. Hartman	Central Plateau near Irazu Volcano	674
Total					5,590



a



b

Fig. 2.—Lateral view of the Camelidae objects.



a



b

Fig. 3.—Top view of the Camelidae objects.

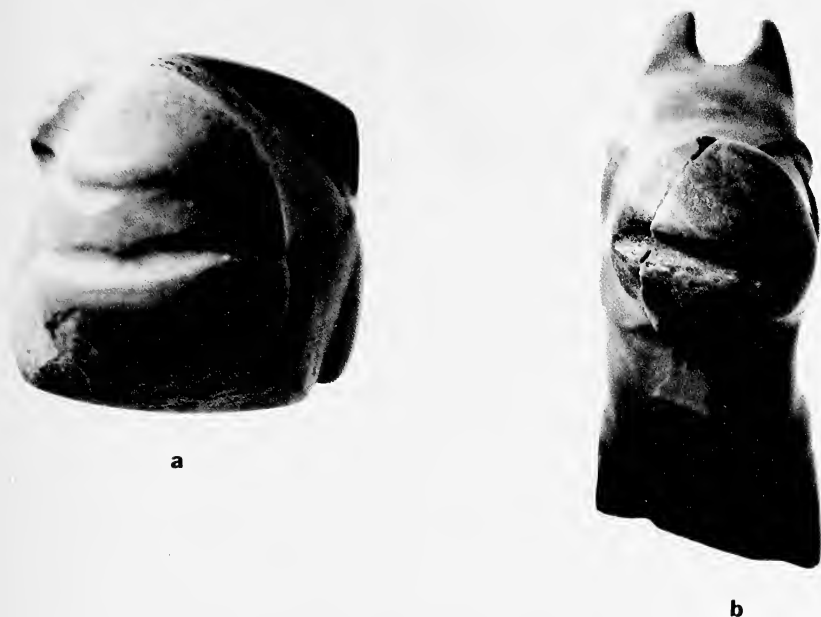


Fig. 4.—Front view of the Camelidae objects.

are well defined and they stand upright on the skull. There is a large bulge in front of the ears and the nose is pronounced. The eyes are formed by incision. The lithic material from which the two camelid heads are manufactured, are native to Costa Rica (Delbert L. Oswald, personal communication).

Otto M. Epping, curator of taxidermy, Carnegie Museum of Natural History, has compared the morphological characteristics of camelids with that of the specimens and he concludes that they closely resemble members of the family Camelidae and not any other species such as deer known for Central or South America.

The American Camelidae (guanaco, *Lama guanicoe*; vicuna, *Lama vicugna*; llama, *Lama glama*; alpaca, *Lama pacos*) are widespread in South America. Both the llama and guanaco had an historic distribution throughout the Andes, from southern Colombia to Chile; the vicuna from southern Ecuador to Chile; the alpaca from southern Peru to northern Argentina (Gilmore, 1950:441, 443, 447, and 451). The llama and guanaco are so close in skeletal morphology that it is almost impossible for the paleozoologist to separate the two (Gilmore, 1950; Wing, 1972; Pires-Ferreira et al., 1976). On the basis of the available

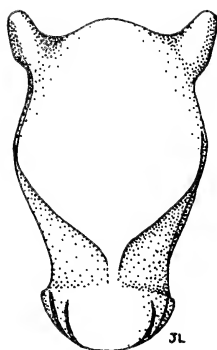
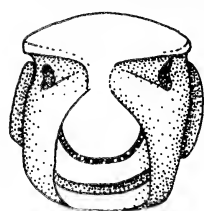


Fig. 5.—Front and top view of object no. 14, Camelidae head.

archaeological evidence, intensive utilization of camelids began by 5500 B.C. and by 2500 B.C. domesticated camelids appear in the Puna de Junin sequence of Peru (Pires-Ferreira et al., 1976). Camelids have also been recovered from Mito phase levels at the Kotosh site on the eastern slopes of the Andes, dating to 1950 B.C. (Wing, 1972).

On the north coast of Peru, there is faunal evidence of camelid herding at two large Sechura period sites (500 B.C. to 500 A.D.) just north of Talara and the portrayals of camelids on Moche vessels (200 B.C. to 600 A.D.) indicates that camelid herding was an important economic element on the Peruvian north coast. The early Spanish accounts of the Department of Piura make note of huge herds of llamas in the Chira and Piura river valleys.

In addition to the two camelid heads, the other camelid represen-

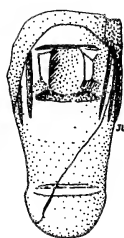
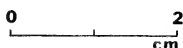
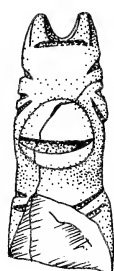


Fig. 6.—Front and top view of object no. 13, Camelidae head.

tations from Costa Rica include an El Bosque period camelid effigy vessel dating to 300 A.D. from the Linea Vieja region (Snarskis, 1975: 11–12; 1976:349–350). Snarskis (1976:350) states that he has seen camelid effigy pots in Costa Rica with burdens on their backs. Fischer (1882:187, Plate 8) also illustrates a camelid head of stone from north-western Costa Rica. The modeling in clay of a camelid by a Panamanian chief for the Spanish and the fact that he related to the Spanish that they were used as beasts of burden, reflects knowledge of llamas in Central America during the sixteenth century (de las Casas, 1961:291).

CENTRAL AMERICAN–SOUTH AMERICAN CULTURAL CONTACTS

It is not our purpose to present a lengthy discussion of Mesoamerican–South American cultural contacts, as reflected in the artifact rec-

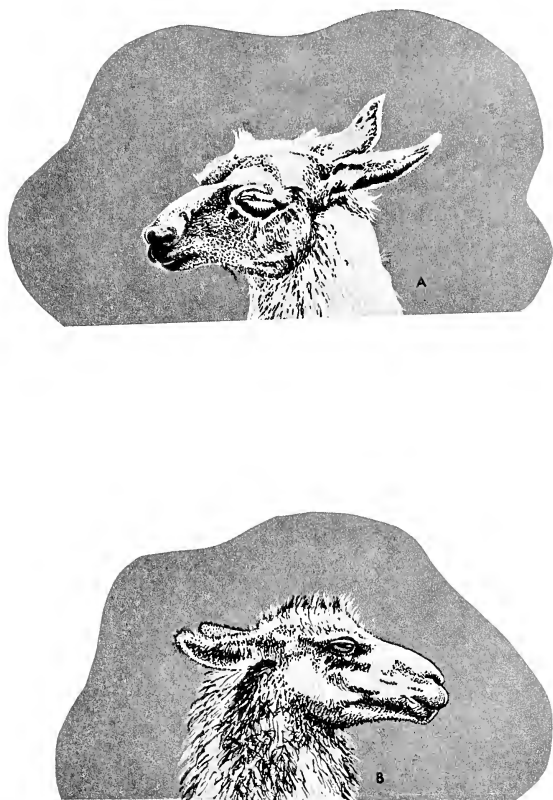


Fig. 7.—Two lateral views of a llama (*Lama glama*).

ord. It is becoming clear that intensive contacts between these two regions began at least by 4000 B.C., and probably earlier (Coe, 1960; del Solar, 1966; Lathrap, 1966, 1975; Lowe, 1975; Meggers, 1964, 1966; Meggers and Evans, 1969; Paulsen, 1974, 1977; Stothert, 1977). The contacts, as evidenced in ceramic stylistic similarities, shaft tombs, metallurgy, and plant domesticates began at least by 4000 B.C. and continued to Spanish contact on the west coasts of Mexico and Central America. These contacts appear to have originated on the coasts of Ecuador and northern Peru.

On the basis of ethnohistoric sources, the Peruvian north coast to Manabi, Ecuador, was the main zone for the extensive use of the large balsa cargo rafts (West, 1961; Edwards, 1965; Lothrop, 1932; Nelson, 1961; Estrada, 1955; Means, 1942). The great balsa raft trade from the Guayas basin to Mesoamerica was well established at the time of Spanish contact. In 1527, Bartolome Ruiz de Estrada, Pizarro's pilot, en-



Fig. 8.—Fragment of mirror back, Izapan style, object no. 1.

countered a balsa raft under sail, carrying 30 tons of goods off the coast of Ecuador. The balsa had left Tumbes on the Peruvian north coast and was heading northwest (Means, 1942:124). The legend of Tupac Yupangui's voyage on balsa rafts from the Guayas basin to two islands, 100 leagues off-shore in 1480 A.D., may have been based on an historical event (Means, 1942:122–123). In addition, the legendary founder of the Lambayeque dynasty, Namlap, who entered the valley on a fleet of balsa rafts from the south during the Early Intermediate Period, is now thought to have some basis in fact (Donnon, 1976:89–91).

The illustrations of balsa and reed rafts on Moche pots provides evidence that coastal navigation had been developed at least by 200 B.C. The vessels are decked and many of them carry goods and sup-

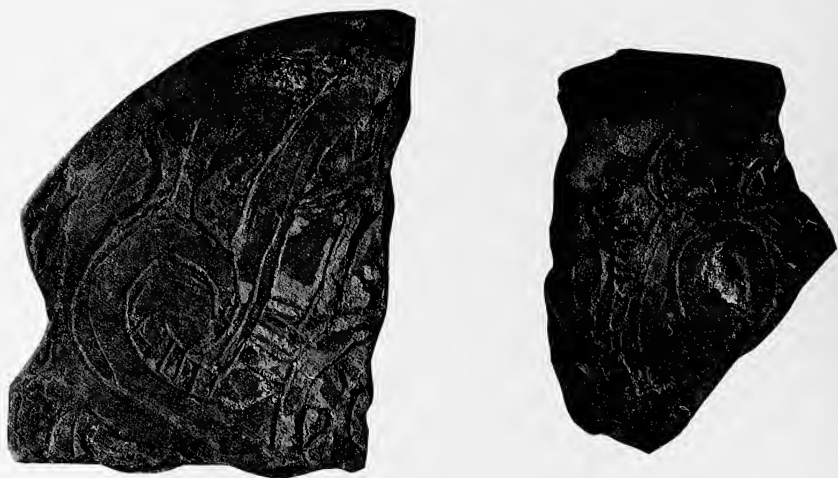


Fig. 9.—Fragment of mirror backs, Izapan style, object no. 2.

plies to support the crews on their voyages (Benson, 1972; Donnon, 1976).

There are also scenes of sea lion hunting on Moche vessels and reed boats on the islands off the north Peruvian coast (Hutchinson, 1950: Plate 8). Kubler (1948:49) illustrates a large collection of Moche wooden figurines from the Lobos Islands, at the southern edge of the Sechura Desert which Hutchinson (1950:49) feels are not from the Lobos Islands, because these islands did not have high grade guano deposits. The assumption that the Moche state was mining guano to use for fertilizer, has never been demonstrated archaeologically. The main factor in the use of the off-shore island was most plausibly for the killing of sea lions and not for the guano deposits. For example, in 1790, the English whale ship *Emilia* stopped at the Lobos Islands and killed 30,000 seals for oil (Stackpole, 1972:129).

Lathrap (1975:53) has made a strong case for Ecuadorian cultural influences in Mesoamerica and has raised the possibility of actual colonization of parts of West Mexico by Ecuadorian migrants. Meggers (1967) has also demonstrated that between 500 B.C. and 500 A.D. the Ecuadorian coast was under strong Mesoamerican influence. This all appears to reflect pattern that has great antiquity.

Bushnell (1951:136) has stated that the close similarities between Guangala pottery of Ecuador and Costa Rica “. . . is so close that I regard it as strong evidence that there was direct contact between the two cultures, probably through migration by sea.”



Fig. 10.—Fragment of mirror backs, without designs, objects no. 3-9.

Based upon similarities between Costa Rican and Ecuadorian ceramic complexes, Allison Paulsen (1977:152) feels that peoples of southern coastal Ecuador and the Guanacaste Province and Nicoya Peninsula of Costa Rica were in contact by sea. The white on red bowls of the Guangala 1 complex of Ecuador were introduced to Costa Rica between 100 B.C. and 100 A.D., whereas in the succeeding Guangala 2 through Guangala 5 periods, bichrome and polychrome wares were introduced to Ecuador from Costa Rica as a result of trade.

Karen Stothert (1977) has documented cultural contacts between Ecuador and Panama during the preceramic period. Based on similarities on the burial patterns of the Vegas complex (4000-6500 B.C.) in Ecuador and that of Cerro Mangote in Panama, she proposes that a cultural interaction sphere was well established by the fifth millennium B.C., that included the 1400 km coast from northern Peru to Panama. Following the preceramic period, there is increasing evidence that the Valdivia and Machillalia complexes of Ecuador were in contact with Central American and western Mexican populations (for example, Paulsen, 1977; Lowe, 1975).

Tantilizing as these data are, we do not understand the nature of the contacts, the types of watercraft involved, or the impact that these contacts had upon the receiving populations. Except for portrayals on Moche pots of rafts the lack of direct archaeological evidence of water-

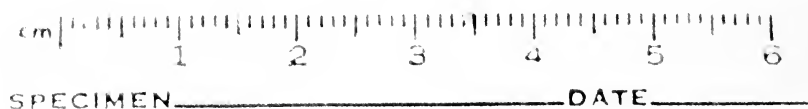


Fig. 11.—Early Classic Maya Jadeite pendant, object no. 11.

Table 3.—*Measurement of Mayan influenced artifacts from Costa Rica.*

No.	Carnegie accession no.	Length	Width	Thickness	Material	Plate
1	2939-1630	6 cm	6 cm	0.3 cm	Slate	8
2	2939-1629	6.7 cm	4.8 cm	0.5 cm	Slate	9
	2939-1629	9.9 cm	7.2 cm	0.5 cm	Slate	9
3	2939-1631	11.2 cm	7.4 cm	0.5 cm	Slate	10
4	2939-1633	12.6 cm	4.2 cm	0.8 cm	Slate	10
5	2939-1632	7.3 cm	6.4 cm	0.5 cm	Slate	10
6	2793-12	5.8 cm	5.1 cm	0.4 cm	Slate	10
7	2939-1128	5.4 cm	2.5 cm	0.4 cm	Slate	10
8	2939-1180	4.3 cm	0.8 cm	0.3 cm	Slate	10
9	2939-1127	5.5 cm	2.7 cm	0.4 cm	Slate	10
10	2939-1628	5.5 cm	4.5 cm	0.9 cm	Jadeite	11, 12
11	2939-1270	3.5 cm	2.4 cm	0.8 cm	Steatite	13a, b
12	2939-1273	3.1 cm	1.9 cm	1.8 cm	Steatite	13c

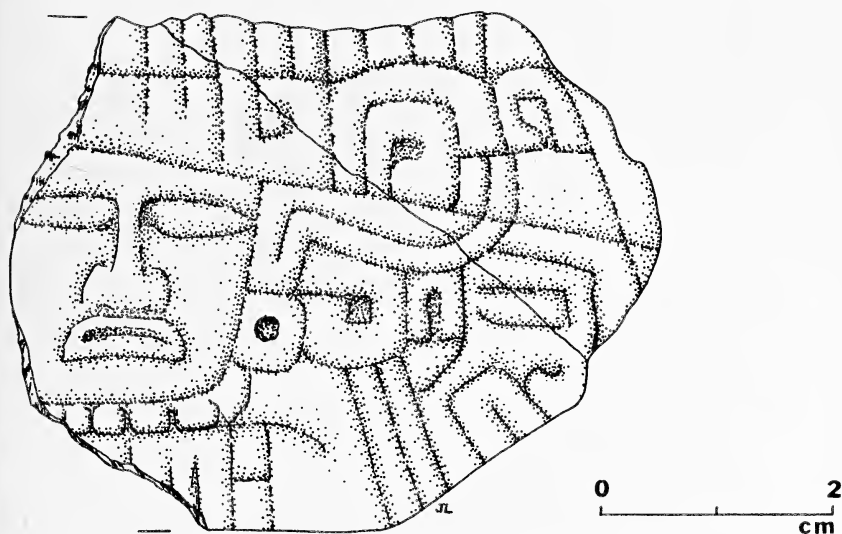


Fig. 12.—Early Classic Maya Jadeite pendant, object no. 11.

craft is not startling, when one compares the scant data for prehistoric water travel with the artifact evidence for extensive use of the west coast of South America by the American whaling industry. Between 1790 and 1870 A.D., the ports of Paita and Tumbes, on the Peruvian north coast, were resupply ports for one hundred to two hundred whaling ships a year. Of the 10,000 whaling voyages made to the Pacific during this period there is almost no artifactual evidence, other than the historical record, to suggest that whaling had any impact on the economies of west coast South American ports (Richardson and Zamecnik, 1977).

MAYAN CONTACT AT LAS HUACAS

Twelve artifacts from Las Huacas can be attributed to Mayan influence. Nine of the objects are mirror backs, and the others are one bead, a face pendant, and a small reptile effigy (see Table 3 for measurements).

The only mirror backs that have designs are numbers one and two, which have U shaped incisions comparable to the Izapan style (Figs. 8, 9). The remaining seven mirror backs are plain with holes drilled in them to be used as pendants (Fig. 10).

The half of a jadeite pendant (no. 10 and Figs. 11, 12) with a low relief face, circular earplugs, elaborate scrollwork and necklace ornaments, was reported by Coe (1962:177). This specimen closely par-

**a****b****c**

Fig. 13.—(a) and (b) are the faces at both sides of object no. 10, steatite bead; (c) small reptilian effigy resembling the Classic Maya "dragon," object no. 12.

allels the early Classic Maya jade specimens illustrated by Rands (1965:571).

A steatite bead (no. 11 and Fig. 13a-b), biconically drilled, with low relief heads on both sides has Maya characteristics (Michael Coe, personal communication).

The last object (no. 12, Fig. 13c) is a reptilian-like figure with typical upturned snout of the Itzmana style (Michael Coe, personal communication) resembling the "dragon" of the classic Maya ceremonial bars. The piece is broken at one end and probably has a duplicate representation of the dragon motif.

Mayan mirror backs and pendants are also present in Costa Rica at the site of La Fortuna in the Atlantic area (Baudez and Coe 1966). The La Fortuna site has the same pottery sequence as that of Las Huacas—zoned bichrome, linear decorated, and early polychrome periods.

CONCLUSIONS

The Nicoya Peninsula of Costa Rica is an important region in regards to cultural contacts with South American and Mayan cultures, for it is here that voyagers from the south and north might have made a significant landfall.

The camelid heads and Mayan derived artifacts at Las Huacas are further suggestions of cultural contacts with the west coast of Mesoamerica by South American cultures and vice-versa.

Wiley (1962) and Lathrap (1974) have argued that the earliest Andean and Mesoamerican states share a common cultural base. The hypothesis that cultural interchanges between South and Mesoamerica gave rise to New World states, must be given serious consideration, for in the past few years ample evidence has been unearthed to demonstrate that far-flung regions were in contact with each other at least by 4000 B.C.

ACKNOWLEDGMENTS

We wish to express our gratitude to Michael D. Coe for his evaluation of the Maya items from Las Huacas; to Claude Baudez for his comments on various aspects of the Hartman collection; to Delbert L. Oswald of the Carnegie Museum for identification of the stone; and to Otto M. Epping, Curator of Taxidermy of the Carnegie Museum for his aid in the identification of the two stone heads as camelids. Special thanks is extended to James L. Swauger, Senior Scientist—Anthropology of the Carnegie Museum of Natural History, for his encouragement and support of the senior author's analysis, over the past two years, of the Hartman collection. Thanks are also due to Jennifer Loynd for preparation of Figures 5, 6, 11; to James Senior for Figures 1 and 7, and to Mark McConaughy for preparing the photographs of the objects.

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DISTRIBUTION, VARIATION, AND SYSTEMATIC STATUS OF *ZYGASPIDIS VIOLACEA* (PETERS) (AMPHISBAENIA: REPTILIA) ENDEMIC TO SOUTHEASTERN AFRICA

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ABSTRACT

Zygaspis violacea (including *vandami* FitzSimons) ranges from southeastern Rhodesia through extreme southern Mozambique to Zululand and into the northeastern Transvaal, South Africa. Examination of the skull and other aspects indicates that *violacea* belongs in *Zygaspis* with *niger* and *quadrifrons*, rather than in the South American genus *Amphisbaena*.

INTRODUCTION

Amphisbaena violacea was briefly described by W. C. H. Peters in 1854 from Inhambane and Lourenço Marques (now Maputo), Mozambique. Measurements for two specimens were provided, but when a more comprehensive description was published (Peters, 1882), data for four individuals were given.

When the latest check list of Recent amphisbaenians (Gans, 1967) went to press, the species *violacea* was retained, with some question, as the only African representative of the otherwise exclusively American genus *Amphisbaena* Linné. The other African species once placed in *Amphisbaena* (Loveridge, 1941) had during the preceding three de-

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cedes gradually been shifted into the distinct genera *Chirindia*, *Cynisca*, *Loveridgea*, and *Zygaspis* (Laurent, 1947; Vanzolini, 1951a, 1951b). However, Vanzolini (1951a, 1951b) retained the species *violacea* Peters in *Amphisbaena*. It is now considered to belong in the genus *Zygaspis* Cope, differing from its congeners principally in having the preocular scales fused with the prefrontals. *Zygaspis violacea* was not included by Saiff (1970) in his study of geographical variation in the genus *Zygaspis*. Although the name has appeared in various lists and has been mentioned in passing (Duméril, 1861; Strauch, 1881; Duméril and Bocourt, 1882; Thominot, 1887; Sclater, 1898; Hewitt, 1910; Werner, 1910; Monard, 1931; Battersby, 1950), the form has never been reviewed.

Amphisbaena vandami was described by FitzSimons in 1930 from a single specimen from Louws Creek in the eastern Transvaal, South Africa. FitzSimons (1943) placed it as a subspecies of *A. violacea*. Loveridge (1941) first placed *vandami* in the synonymy of *A. violacea*, but subsequently (Loveridge, 1951) accepted it as a subspecies of that form. Recent collections have extended the range of *violacea* northward into Rhodesia and southward into central Zululand. Boulenger (1910) had erroneously extended the range of this species to Botswana by placing *A. capensis* Thominot in the synonymy of *A. violacea*, instead of *A. quadrifrons* (Loveridge, 1941).

We are grateful to the following curators of institutions (identified throughout by the abbreviations given in parentheses) for permission to examine or borrow material in their care: Carl Gans Collection, Ann Arbor (CG); Sara Manaças and M. Pinheiro, Centro de Zoologia, Lisbon, Portugal (CZL); J. P. Tello Collection, Maputo, Mozambique (JPT); Dr. U. de v. Pienaar, Kruger National Park, South Africa (NKW); Dr. J. A. Pringle, Natal Museum (NMP); Mr. W. D. Haacke, Transvaal Museum (TM); Umtali Museum (UM); Dr. G. Peters, Zoologisches Museum, Berlin, D.D.R. (ZMU). Specimens have been deposited in Carnegie Museum of Natural History (CM). Tony and Elsa Pooley helped obtain specimens and we are grateful for their hospitality at Ndumu and St. Lucia. Supported by NSF BMS DEB 76 18289.

COMMENTS ON THE LOCALITIES

Zygaspis violacea has been recorded from twenty-five localities. In the Gonarezhou National Park, southeastern Rhodesia, specimens were found under logs lying on red aeolian Cretaceous sands where there was termite activity. The two individuals from Gorhwana Pan were under stones forming a boundary beacon. The Mozambique and Zululand localities are all in alluvial soils of the coastal plain. The habitats occupied by the Ndumu specimens were described and illustrated by Pooley et al. (1973). The specimens from the southeastern Transvaal, South Africa, occurred on a variety of substrates. The Pumbe Sandveld, which supports a population of *Z. violacea*, is Kalahari sand, although the similar Nyandu Sandveld area on the north-

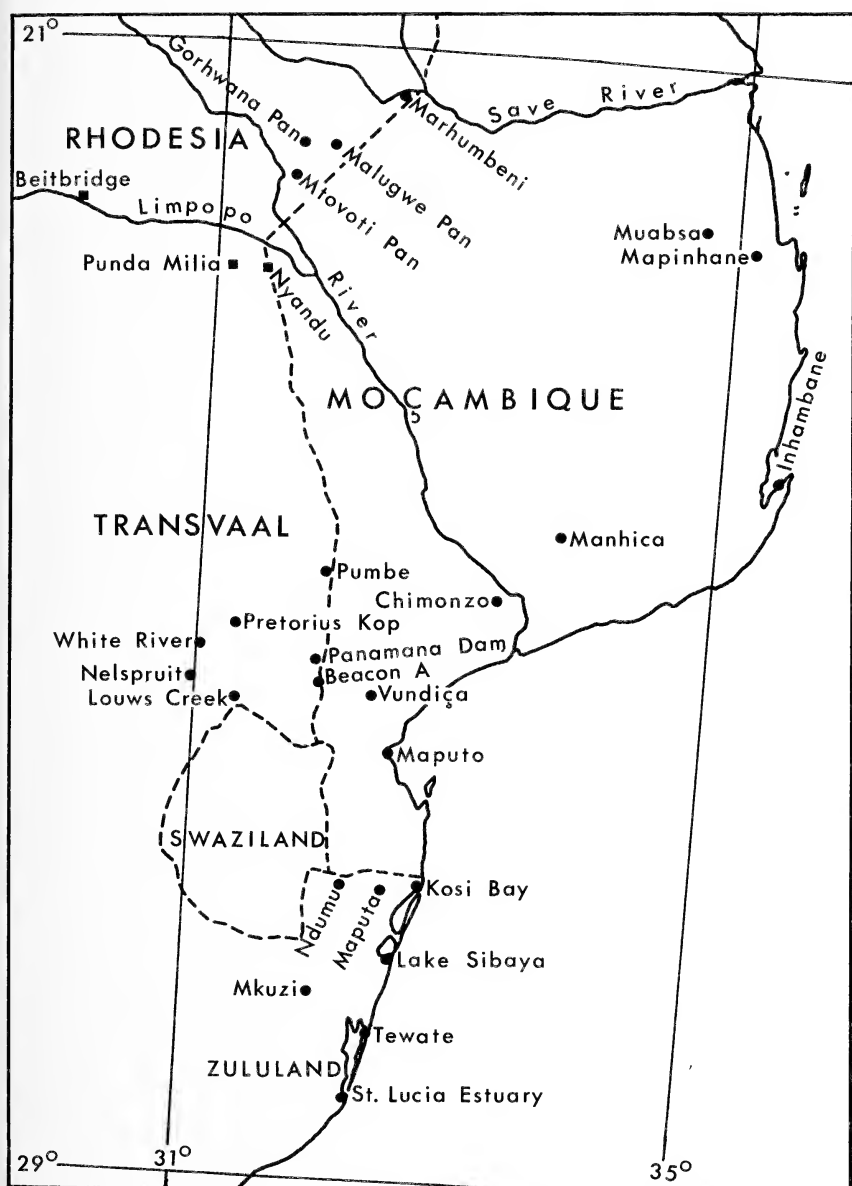


Fig. 1.—Map showing localities for *Zygaspis violacea* (solid circles) and adjacent localities for *Z. quadrifrons* (solid squares).

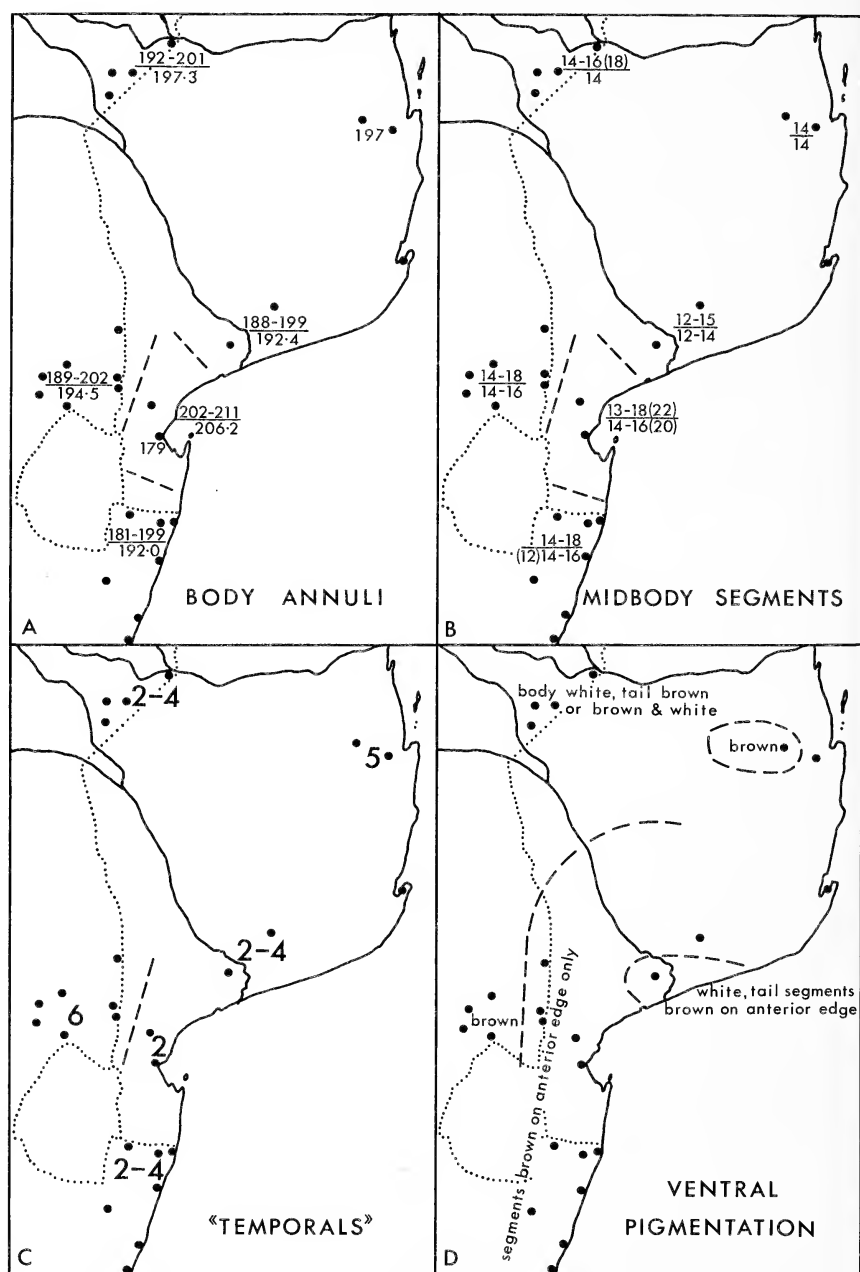


Fig. 2.—*Zygaspis violacea*, summary of geographical variation. A) Number of body annuli—range of variation above the line, mean for the area below the line. B) Number

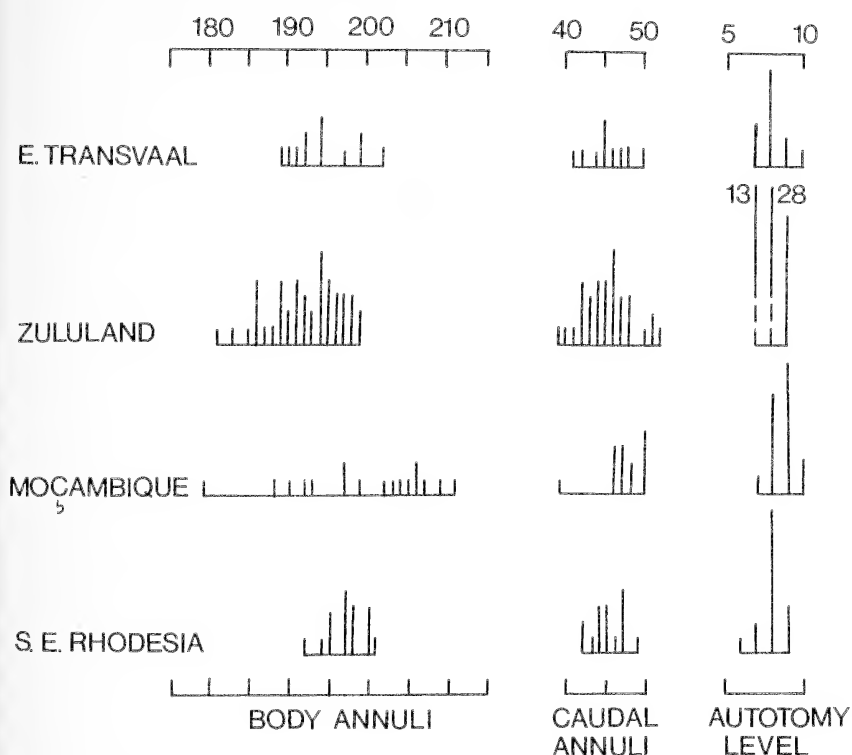


Fig. 3.—Diagram showing frequency distribution for number of annuli and position of autotomy annulus for four geographic areas.

eastern boundary of the Kruger Park is inhabited by *Zygaspis quadrifrons* (Fig. 1). The other material from the southeastern boundary of the Kruger Park is from the rhyolite formations of the Lebombo Range. The specimens from Pretorius Kop, White River, Nelspruit, and Louws Creek are all from granite areas on the lower slopes of the eastern escarpment (maximum altitude about 900 m at White River), the vegetation being lowveld savanna. Specimens were found on granite and rhyolite outcrops by turning over stones in shaded areas (Pienaar, 1966).

of segments to a midbody annulus—dorsal above the line, ventral below the line, rare variations in parentheses. C) Total number of shields in the temporal region (postoculars + temporals + postsupralabials). D) Ventral pigmentation.

GEOGRAPHICAL VARIATION

The localities from which specimens of *Zygaspis violacea* have been recorded are mapped in Fig. 1. Geographical variation was noted in four characters and mapped and graphed in Figs. 2 and 3.

The number of body annuli is highest at Maputo/Vundica (range = 202–211, mean = 205.9) and lowest in Zululand (range = 181–199, mean = 192.1), all other areas having counts in the range 188–202 (Fig. 2A). The mean of the combined Rhodesia sample (197.3) is higher than that of Transvaal specimens (194.4), but the obvious intrasample variation suggests that some of the differences reflect differential sampling of microgeographic populations (Fig. 3). Thus, UM 7600, collected at Maputo in 1964, has only 179 body annuli, in sharp contrast to the other Maputo specimens (collected in 1916), which have 202–211 body annuli. It appears that two different populations have been sampled, but we do not know whether they are separated by time or space.

The number of midbody segments is highest in the south (usually 14–18/14–16), but UM 7600 from Maputo is again unique, having 20–22/18–20 segments. The lowest counts are at Manhica (12–15/12–14). Specimens from Chimonso, Mapinhane, and Muabsa all have 14/14. The Rhodesian specimens have intermediate counts, usually 14–16/14 (Fig. 2B).

The 'temporal' arrangement with the most and smallest segments, shown by the type of *A. vandami* (FitzSimons, 1930:Fig. 13; 1943: Fig. 259), comprises anterior and posterior postoculars, anterior and posterior temporals and anterior and posterior postsupralabials, a total of six shields. This arrangement is found only in the eastern Transvaal (Fig. 2C). Elsewhere the number of shields is reduced to two to four. Usually the sequence is for the anterior and posterior temporals to fuse (UM 28457, Mapinhane), then the two postsupralabials, giving the $2/1/1 = 4$ formula, which is common in Zululand (Fig. 4). The two postoculars may also fuse to give a $1/1/1 = 3$ formula, or the postsupralabials may be fused with the temporals to give $2/1/0 = 3$. These formulae are rare. The final stage is reached in 'typical' *violacea*, with a single postocular over a single temporal, that is $1/1/0 = 2$. This formula is usual in specimens from Maputo, and is common elsewhere in Mozambique, Rhodesia, and Zululand (Fig. 5).

The uniform brown dorsal pigmentation shows no geographical variation, but there is considerable variation in ventral pigmentation (Fig. 2D). Specimens from Louws Creek, Nelspruit, and Pretorius Kop are uniform brown apart from the chin, which is white (sometimes a few white ventral patches anteriorly). Similar pigmentation is found in the single Muabsa specimen. The specimens from Zululand, eastern border of the Kruger Park, and most Mozambique localities have each

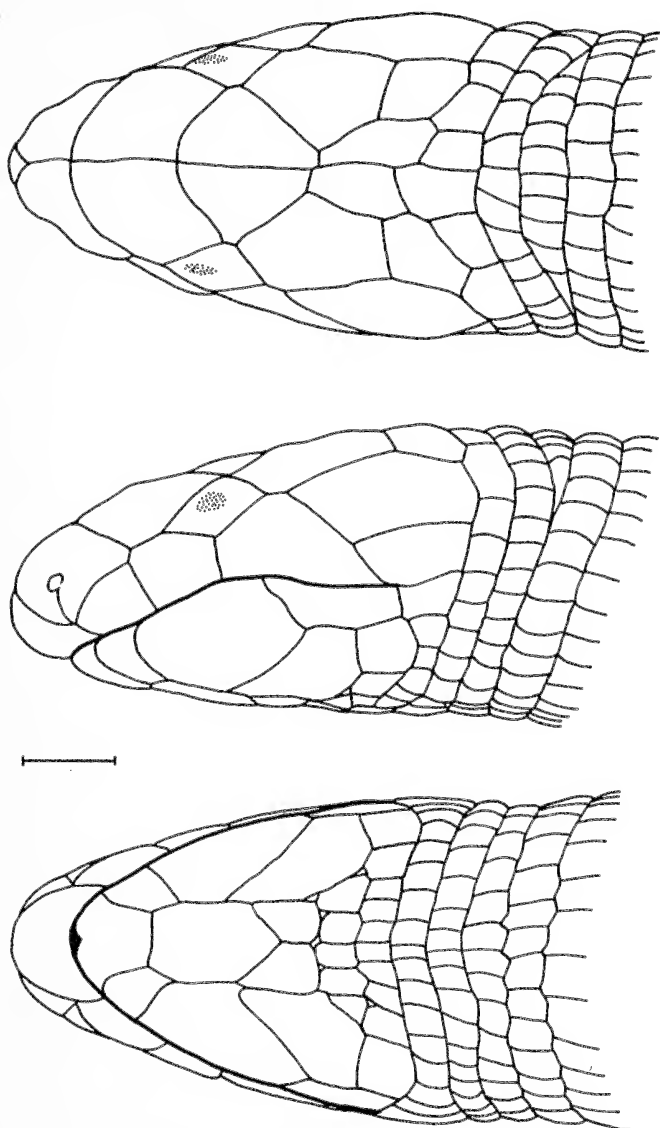


Fig. 4.—*Zygaspis violacea*. Dorsal, lateral, and ventral views of the head of CM 65877 from Mkuzi Game Reserve, Zululand, to show the condition with relatively few temporal segments. The line equals 1 mm to scale.

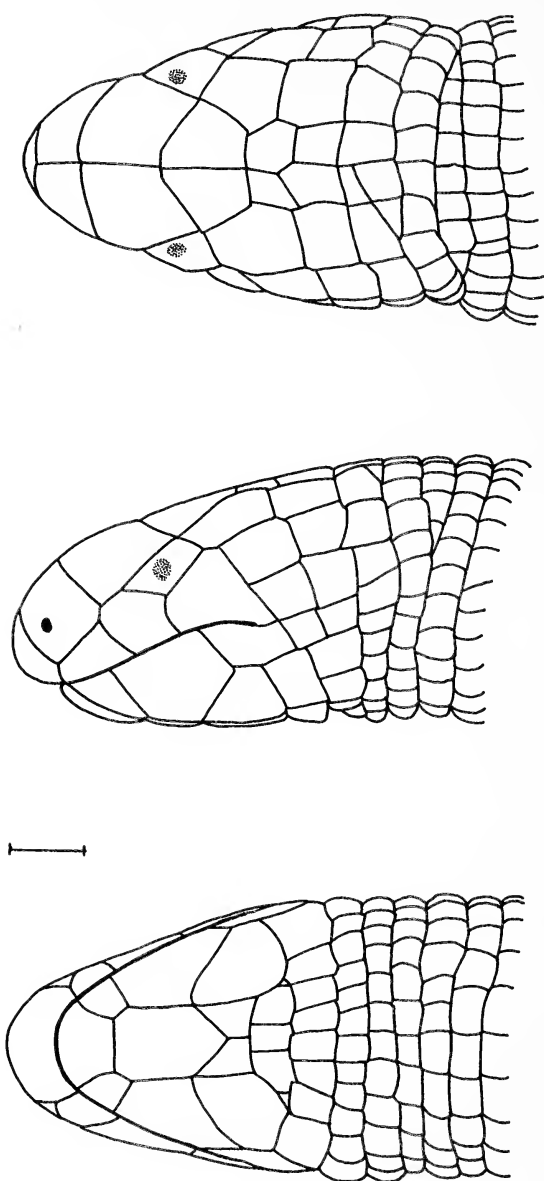


Fig. 5.—*Zygaspis violacea*. Dorsal, lateral, and ventral views of the head of NKW 192a from Shabene Kop, near Pretorius Kop, Kruger Park, South Africa, to show the condition with relatively many temporal segments. The line equals 1 mm to scale.

ventral segment brown anteriorly, covering as much as half the segment. The Chimonso specimen is unique in having this pattern on the tail only, the body annuli being uniform white below. Rhodesian specimens also have the body annuli uniform white, but the ventral tail annuli may be uniform brown or show an irregular mosaic of brown and white segments.

TAXONOMY

Amphisbaena vandami FitzSimons was based on a single specimen (from the Barberton district), which lies at one end of the range of variation within *Z. violacea*. The Maputo and Kosi Bay material, which FitzSimons had for comparison, lies at the other extreme. The stouter head and less prominent snout of western specimens may reflect adaptation to harder substrates encountered on the escarpment, other populations occur in sandy alluvial soils. The short frontal suture of the holotype of *vandami* is not matched by any other specimen, despite great variation in the relative length of this suture. The six 'temporals' of *vandami* contrast strongly with the two shields of the Maputo and Kosi Bay specimens, but subsequently collected material shows a range of intermediate conditions. The differences in numbers of body annuli and segments per annulus have been effaced by additional material. Our analysis of geographical variation provides no grounds for retention of *vandami* as a subspecies.

GENERIC STATUS

The species *Amphisbaena violacea* was retained in the genus *Amphisbaena* by Vanzolini (1951a, 1951b), although he had no material, because Peters' (1882) small figures of the skull "show that it agrees very closely with the South American forms of the *A. darwini* group" and presumably because its cephalic segmentation conformed with the "New World pattern" (that is, with that of the genus *Amphisbaena* otherwise restricted to the Americas). However, in the same papers Vanzolini recognized the genus *Zygaspis* (his *Shrevea*) as generically distinct, based upon dissection of a specimen of *Z. quadrifrons* (from the Congo = Zaire), and justified by the occurrence of an "enlarged proximal portion of the quadrate," the "peculiar postorbital arch and the characteristic sutures of the snout . . . and . . . the cephalic scutellation."

Vanzolini's manuscript provides only limited amplification of these statements. Consequently we checked his description by dissection of the skulls of two specimens each of *quadrifrons* and *violacea* and one of *Z. niger* (from Angola and Zambia; see Saiff, 1970). All species share the enlargement of the quadrate, as well as the general architecture of this element, which differs from those shown in Vanzolini's

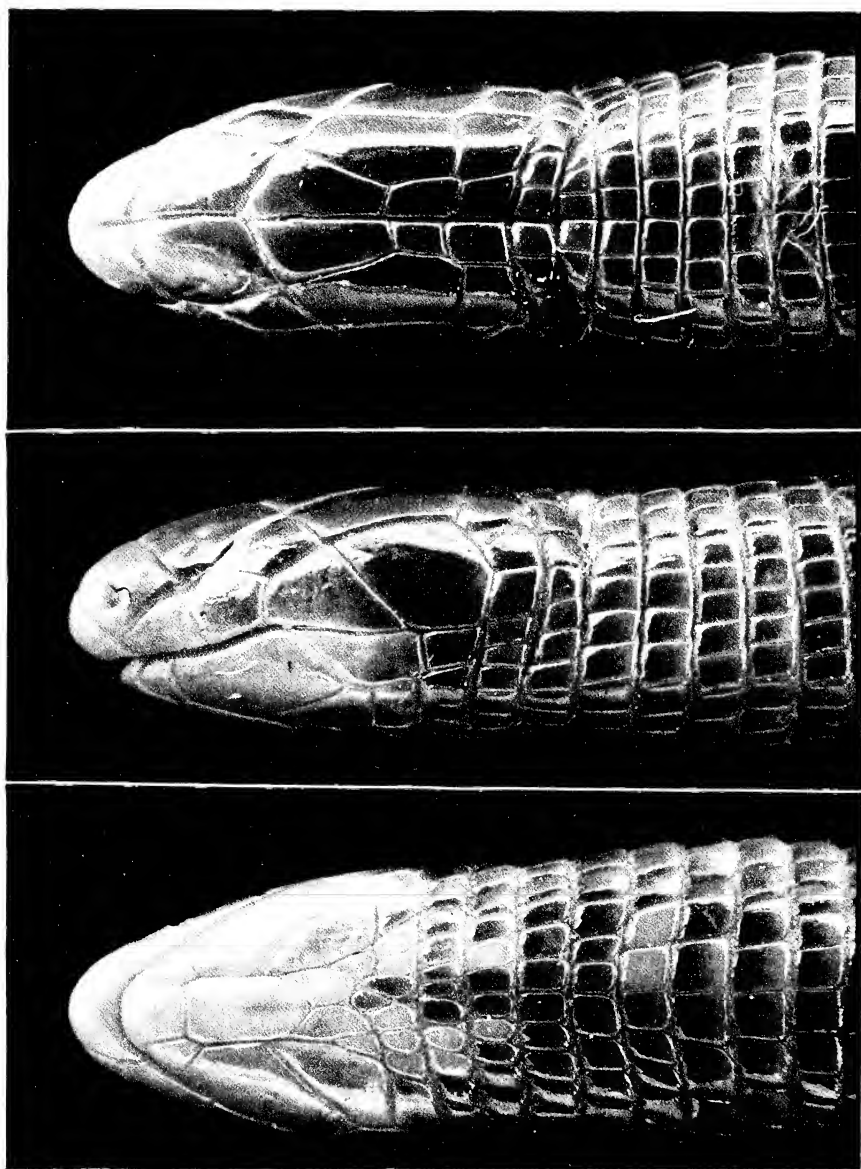


Fig. 6.—*Zygaspis violacea*. Dorsal, lateral, and ventral views of the head of CG 4117 from Ndumu Game Reserve, Zululand, showing the "typical" arrangement of shields in the temporal region.

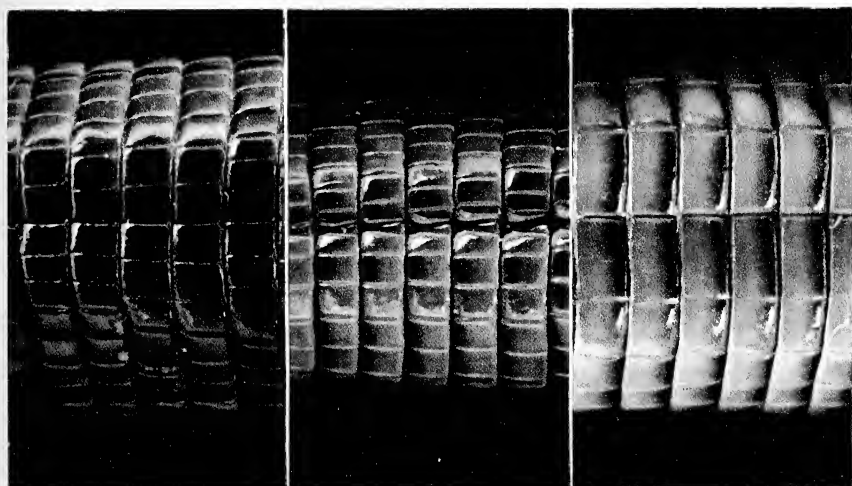


Fig. 7.—*Zygaspis violacea*. Dorsal, lateral, and ventral views (from left to right) of a midbody section of CG 4117 from Ndumu Game Reserve, Zululand, showing size and shape of segments.

illustrations of the skull of various species of *Amphisbaena*. The “peculiar postorbital arch” is equivalent, but less obvious in our specimens of *niger*, *quadrifrons* and *violacea*. The gap is never closed and the condition reminds of that in certain Antillean forms of *Amphisbaena*. The three species, *niger*, *quadrifrons*, and *violacea*, also form the anterior part (snout) of the skull from the premaxilla (in a pattern reminiscent of some Antillean forms of *Amphisbaena*, Gans and Alexander, 1962).

The diagnostic character in the cephalic scutellation is separation of the prefrontals into “prefrontal” and preocular segments. Their fusion (or absence of separation) in the smaller *violacea* reduces the number of cephalic segments to that seen in typical *Amphisbaena*. However, the scale proportions of *niger*, *quadrifrons* and of *violacea* agree among each other, but differ from those seen in the genus *Amphisbaena*. The two to three sets of parietal segments are subequal in size and significantly smaller than the frontals, providing a medial zone of segmental enlargement. The segments of the cheeks (whatever their architectural details) are significantly enlarged far beyond the zone in which enlargement (or segmental fusion) takes place in *Amphisbaena*, and reminiscent of the condition further developed in *Chirindia* (Broadley and Gans, 1978). In summary, the narrowly allopatric species *quadrifrons* and *violacea* are certainly congeneric with each other and with *niger*. There are enough differences from the relatively small

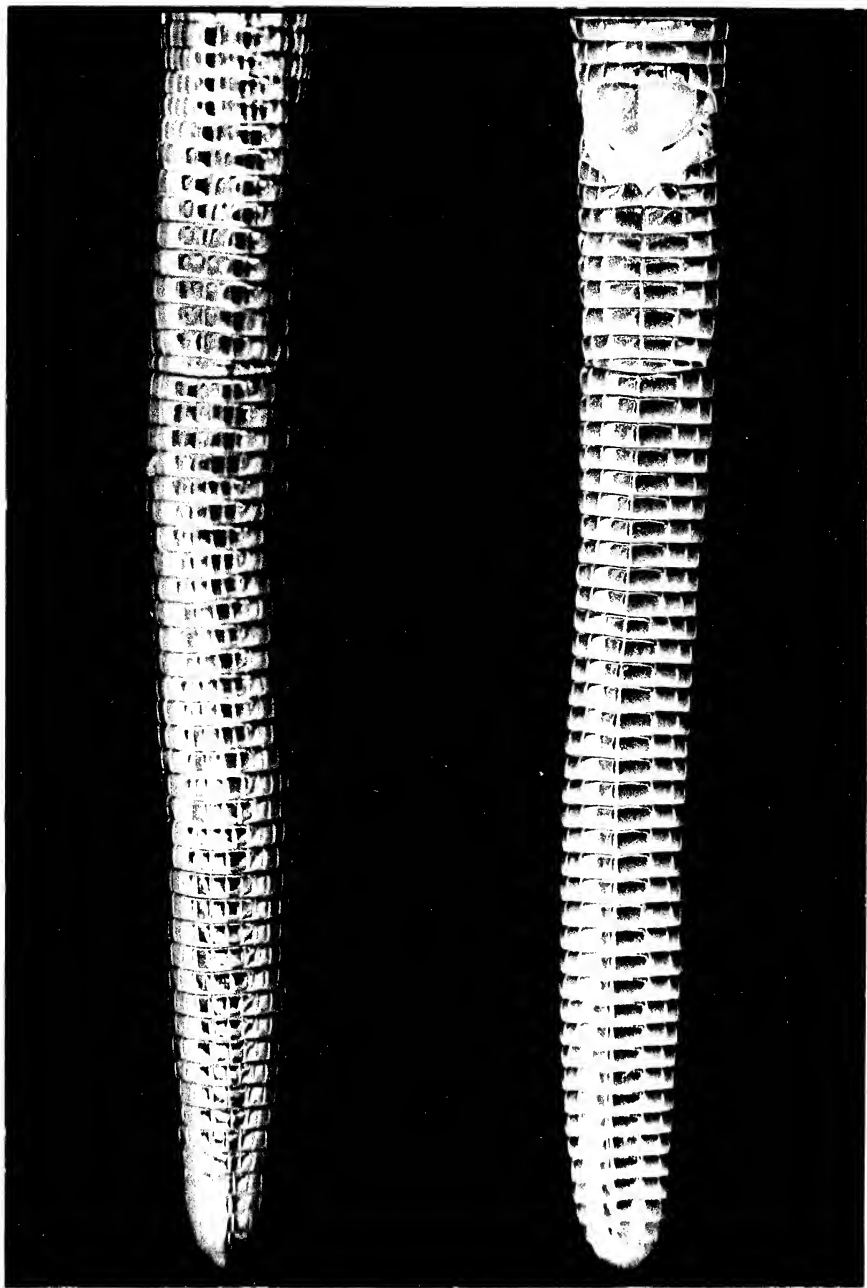


Fig. 8.—*Zygaspis violacea*. Dorsal and ventral views of the cloacal region and tail of CG 4116 from Ndumu Game Reserve, Zululand.

sample of *Amphisbaena* examined for comparison to maintain these three species in the separate genus *Zygaspis* until an overall review of the generic affinities in the family can be completed.

KEY TO THE SPECIES OF THE GENUS *ZYGASPIIS*

- 1a. A pair of discrete preoculars separate the prefrontals from the oculars . . . 2.
- 1b. Preoculars fused with prefrontals *violacea*.
- 2a. Third supralabial bordered by a temporal shield superimposed on a smaller postsupralabial; uniform brown above, paler below *quadrifrons*.
- 2b. Third supralabial bordered by a single large temporal shield; each segment on body and tail black anteriorly, white posteriorly (dorsal segments 50 to 90% black; ventral segments less than 50% black) *niger*.

SYSTEMATIC ACCOUNT

Zygaspis violacea (Peters)

Amphisbaena violacea W. C. H. Peters, 1854:620. Type-locality: "Inhambane, Lourenço-Marques" (=Maputo), Mozambique. Syntypes: ZMU 4814 (Inhambane), ZMU 9420 (Maputo).

Amphisbaena vandami FitzSimons, 1930:32. Type locality: Louws Creek, Barberton District, eastern Transvaal. Holotype: TM 4279.

Description

A small species of *Zygaspis* with the preoculars fused with the prefrontals, three supralabials and from two to six shields in the temporal region (one or two postoculars; one or two temporals; zero to two postsupralabials). The mental and postmental are followed by two anterior and one to seven (usually four) posterior postgenials (the two anterior often fused with the median two posterior), there are seven to 11 postmalar shields. There are three infralabials.

There are 179–211 annuli on the body and 39–52 (Peters, 1882, records 59) on the tail. The distinct autotomy annulus is the sixth to tenth postcloacal annulus; it may be narrower and darker than adjacent annuli (Fig. 3). A midbody annulus contains 12–22 (generally 14 or 16) dorsal and 12–20 (generally 14 or 16) ventral segments. There are four precloacal pores on the last body annulus, six (rarely four, seven or eight) precloacal and 10 to 18 postcloacal segments. The four median precloacal segments are large, the lateral ones very small. Where there is an autotomy, there is a shrinkage and rounding off of a callus terminal pad, with the segments of the last annulus running into this. Twenty-four % of the specimens examined had autotomized tails, the incidence being highest in Zululand (33%) and lowest in Rhodesia (nil).

The largest complete specimen is UM 17731 from Marhumbeni, Rhodesia, which measures 164 + 32 mm. It is exceeded in snout-vent length by TM 28507 from Lake St. Lucia (185 mm) and NKW 235A from the Pumbe Sandveld (172 mm). There is no geographical variation in size. The smallest specimen (UM 29943) measures 65 + 12 mm. The snout-vent length/midbody diameter ratio varies from 26 to 43 with no geographical significance. The tail is more slender than the body, particularly in juveniles where it is almost one half the diameter of the body. Just posterior to the cloaca the tail narrows markedly, mainly by a lateral narrowing.

Pigmentation.—The rostral, mental, and first infralabials are always unpigmented. The degree of pigmentation of the nasals is variable, but otherwise the entire dorsal surface is uniformly dark, although there may be a tendency for the pigment to be

emphasized on the anterior edges of segments. The ventral pigmentation shows considerable geographical variation (Fig. 2D). In specimens from Zululand and south Mozambique the chin is white, but otherwise most segments are heavily pigmented only on the anterior edge (as in *Z. niger*: Saiff, 1970: Figs. 14–15). The cloacal segments (and sometimes some of the postmalars) are often uniformly white.

Locality Records

Rhodesia (Gonarezhou National Park): Gorhawana Pan, UM 29942–3; Malugwe Pan, CM 65879–65880, UM 12198, 12275, 12318, 12335–7; Marhumbini, UM 17671–2, 17731–2; Mtovoti Pan, UM 17777. *Mozambique*: Chimonso, TM 29386; Inhambane (Peters, 1854, 1855, 1862, 1882; Boulenger, 1885; Bocage, 1896; Lichtenstein, 1856; Loveridge, 1941; Gans, 1967), ZMU 4814 (syntype, not seen); Manhica (Manaças, 1957), CZL 524–7; Mapinhane, UM 28457; Maputo, formerly Lourenço Marques (Peters, 1854, 1855, 1862, 1882; Bocage, 1896; FitzSimons, 1930, 1943; Loveridge, 1941; Gans, 1967), CG 1818, CM 65882, NMP 1374, TM 2921–2923, 3000, 3358, 3404, ZMU 9420 (syntype, not seen); Muabsa, JPT 575; Vundica, TM 29454–29455. *South Africa* (Zululand): Kosi Bay (Boulenger 1908; FitzSimons, 1930, 1943; Loveridge, 1941), NMP 256, TM 2810; Lake Sibaya Research Station, TM 47975; 15 km W of Maputa, TM 30018–9; Mkuzi Game Reserve (Pooley, 1965), CG 2485, CM 65877–65878; Ndumu Game Reserve (Pooley 1965; Pooley et al., 1973) CG 4057, 4059, 4115–9, 4545–8, 4550–1, 4553, 4557–9, 4565–74, 4576–80, 5264–73, CM 65881, TM 28769, 31300, 34696–7; St. Lucia Estuary, TM 28507, 33611; Tewater, east shore of Lake St. Lucia, TM 45818–20. *South Africa* (Transvaal): Kruger National Park (Pienaar, 1966)—Eastern boundary, beacons A to B, NKW 190, 197A; Panamana Dam, NKW 298A; Pumbe Sandveld, NKW 235A & B; Pretorius Kop, NMP 1486–1487; Shabene Kop, near Pretorius Kop, NKW 192A; Louws Creek (FitzSimons, 1930, 1943; Loveridge, 1941; Gans, 1967), TM 4279 (holotype of *A. vandami*); Nelspruit (FitzSimons, 1943), NMP 789A–789B, TM 39542; White River (FitzSimons, 1943).

Biological Miscellanea

Peters (1882) illustrated the skull, tongue, trachea, lung, and other viscera and Brock (1941) used the description to comment on placement and morphology of the species. The ear and hearing are discussed in Gans and Wever (1972) and Wever and Gans (1973).

Huang and Gans (1971) noted that both *Zygaspis quadrifrons* and *Z. violacea* have six pairs of M and 12 pairs of m chromosomes. This is equivalent to the karyotypes of the Antillean species *Amphisbaena fenestrata* and *A. manni* and differs from that of *Chirindia langi* (M = 6; m = 9–11).

The only record of predation is a specimen found in the stomach of an *Atractaspis bibronii* collected at Muabsa, Mozambique.

Zygaspis violacea is not sympatric with any other small amphisbaenian. Its absence from the northern end of the Kruger National Park may reflect its displacement by *Z. quadrifrons* the range of which stretches eastwards through the Limpopo Basin (Fig. 1). The sandveld habitats in the Gonarezhou Park are very similar to the Nyandu Sandveld. *Zygaspis violacea* does not occur north of the Save River and *Chirindia swynnertoni* has not been taken south of this river (Broadley

and Gans, 1978). Throughout most of its range (Mapinhane south to Sordawana Bay, Zululand), *Z. violacea* is sympatric with the much longer and somewhat thicker amphisbaenian *Monopeltis s. spheorhynchus*, but in the Gonarezhou National Park it is sympatric with the very much stouter *M. leonhardi* and *M. c. capensis* (Broadley et al., 1976).

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PALEONTOLOGY AND GEOLOGY OF THE BADWATER CREEK AREA, CENTRAL WYOMING. PART 15. REVIEW OF THE LATE EOCENE PRIMATES FROM WYOMING AND UTAH, AND THE PLESITARSIIFORMES

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ABSTRACT

New primate material from the late Eocene of Badwater allows documentation of the occurrence and systematics of seven species as follows: *Phenacolemur mcgrewi*; *P. shifrae* (new); *Troglemur* sp.; *Macrotarsius siegerti*; *Chumashius* sp.; *Uintasorex* sp. cf. *U. parvulus*; *Mytonius hopsoni*. *Ourayia*, from the Uintan of Utah, is more strictly defined, with part of the hypodigm referred to *Macrotarsius jepseni* (new combination). The alleged microsyopid affinities of uintasoricines and some paromomyids are reviewed and not accepted. The relationships among plesiadapiform-tarsiiform primates are revised in accordance with inferred shared-derived similarities, and two major clades are recognized—all Plesiadapiformes (Plesiadapidae, Paromomyidae, Microchoeridae, and Anaptomorphidae) share the derived protocone fold on the upper molars; all Tarsiiformes (Omomyidae: Omomyinae, Uintasoricinae) are united in having continuous and parabolic protocristae on the upper molars enclosing a broad, shallow trigon basin.

INTRODUCTION

Since the last review of the late Eocene primates from the Badwater Creek area (Robinson, 1968), continued collecting from the Uintan (localities 5, 5A, 5 Front, 5 Back, Wood, 6) and Duchesnean (locality 20) deposits has yielded additional dental remains referable to new and previously described taxa. It is clear that the Badwater sediments are not part of the Tepee Trail Formation (Krishtalka and Black, 1975; West et al., manuscript) although their formational status has not yet been determined.

Robinson (1968) described seven species of primates from Badwater—one as a paromomyid (*Phenacolemur mcgrewi*), four as omomyids (*Macrotarsius siegerti*, *?Hemiacodon* sp., *?Chumashius* sp.,

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one sp. incertae sedis), and two as anaptomorphids (*Uintasorex* sp. cf. *U. parvulus*, ?*Trogolemur* sp.). In the same paper Robinson also discussed Uintan primates from Utah—*Ourayia uintensis*, *Hemiacodon jepseni* (new species), and *Mytonius hopsoni* (new genus and species), all omomyids.

Uintasorex has since been identified as a microsyopid (Szalay, 1969b; Bown and Gingerich, 1973; Bown and Rose, 1976) although, as discussed below, conclusions concerning the composition and affinities of this family are not without problems. The hypodigm of *Ourayia* has expanded and contracted with each review of the genus, and an attempt to clarify its systematics is made. Also, the anaptomorphids and omomyids as treated by various workers (Simons, 1972; Szalay 1976) do not appear to be monophyletic groups. Continued adherence to these taxonomic schemes precludes a rigorous reflection of the phylogenetic relationships among these taxa. A summary of a new and different view of relationships among the major taxa of Plesitarsiiformes (Gingerich, 1976), based on inferred shared-derived characters, is presented in Fig. 1. A more detailed treatment of all plesitarsiiform genera will appear elsewhere (Krishtalka and Schwartz, manuscript). Accordingly, among the primates recorded here, *Macrotarsius*, *Chumashius*, *Mytonius*, and *Ourayia* (Omomyinae) and *Uintasorex* (Uintasoricinae) are tarsiiforms. *Trogolemur* (Anaptomorphidae) and *Phenacolemur* (Paromomyidae) are plesiadapiforms. Microsyopids are provisionally included in plesitarsiiforms in agreement with Bown and Gingerich (1973), Bown and Rose (1976), and Gingerich (1976), but *pace* Szalay (1975, 1976).

Schwartz and Krishtalka (1976, 1977) have suggested that the antemolar dental complement of plesiadapiform-tarsiiform primates is a canine at the front of the jaw followed by five or fewer premolars. Premolars at the first and third loci may be retained deciduous teeth. This interpretation of dental homologies will be followed here.

←

metacone occurs on P^4 ; paraconid reduced on P_5M_{1-3} ; trigonid quadrate on M_1 , anteroposteriorly compressed on M_{2-3} ; M_3 with prominent third lobe and double or large hypoconulid.

Node 9.—Rudimentary protocone on P^4 ; less robust lower canine; trigonid on M_{1-3} inclined anteriorly.

Included genera are as follows: Microsyopidae (*Cynodontomys*, *Microsyops*, *Craseops*, *Alsaticopithecus*); Plesiadapidae [*Pronothodectes* (*Elphidotarsius*, *Carpodactes*, *Carpolestes*), *Nannodectes*, *Plesiadapis*, *Chiromyoides*, *Platychoerops*]; Paromomyidae [(*Palaeochthon*, *Palenochtha*), (*Paromomys*, *Phenacolemur*, *Zanycteris*, *Picrodus*)]; Microchoeridae (*Nannopithecus*, *Necrolemur*, *Microchoerus*, *Rooneyia*); Anaptomorphidae [(*Loveina*, *Shoshonius*, *Washakius*, *Hemiacodon*), (*Anemorhysis*, *Altanius*, *Pseudotetonius*, *Trogolemur*, *Absarokius*, *Anaptomorphus*, *Tetonius*)]; Omomyidae [(*Uintasorex*, *Niptomomys*, *Tinimomys*), (*Omomys*, *Macrotarsius*, *Ourayia*, *Mytonius*, *Tarsius*, *Chumashius*, *Uintanius*, *Pseudoloris*)].

Abbreviations in this paper are as follows: CM, Carnegie Museum of Natural History; PU, Princeton University; UCM, University of Colorado Museum; YPM, Yale Peabody Museum; L, length; W, width; PW, posterior width.

All measurements in text and in the tables are in millimeters. All photographs in the figures are scanning electron stereomicrographs.

SYSTEMATIC ACCOUNTS

Family Paromomyidae

Phenacolemur Matthew, 1915

Bown and Rose (1976), in the latest review of this genus, resurrected *Ignacius* Matthew and Granger, 1921, to include *I. frugivorus*, *I. fremontensis*, and *I. mcgrewi*—species formerly assigned to *Phenacolemur* (Simpson, 1955; Robinson, 1968; Gazin, 1971)—and a new species, *I. graybullianus*. Retained in North American *Phenacolemur* are *P. praecox*, *P. citatus*, *P. jepseni*, *P. pagei*, and a new species, *P. simonsi*.

Among the many features listed in their diagnoses of the two genera (Bown and Rose, 1976:112, 114), only three appear to be truly diagnostic, that is, not shared. In contrast to *Phenacolemur*, *Ignacius* has the following characteristics: (1) a narrower and deeper mandible relative to the cheek teeth; (2) a V-shaped rather than anteroposteriorly straight centrocrista on the upper molars; and (3) smaller P_4^4 than M_1^1 . However, a number of contradictions between this diagnosis and the morphology of the included species imply that the validity of *Ignacius* is open to question: (1) *I. mcgrewi* has anteroposteriorly aligned rather than V-shaped centrocristae on M^{1-2} —a characteristic of *Phenacolemur*. Neither P_4^4 nor the mandible of this species has been recovered as yet; (2) in *P. simonsi* the centrocristae are straight (*Phenacolemur*-like), but P_4^4 are smaller than M_1^1 (*Ignacius*-like) (Bown and Rose, 1976; Fig. 3b, Table III). The mandible of *P. simonsi* is unknown; (3) in *P. pagei* the centrocristae are straight and P_4 is larger than M_1 (*Phenacolemur*-like), but P^4 is smaller than M^1 (*Ignacius*-like).

If these species do constitute two genera, the diagnostic characters cited by Bown and Rose (1976) are unsatisfactory. *Ignacius* is here provisionally considered valid only on the basis of the V-shaped centrocristae on the upper molars, and thus includes only *I. fremontensis*, *I. frugivorus*, and *I. graybullianus*.

Since Robinson (1968) described *P. mcgrewi*, additional teeth of this and a new, smaller species have been recovered from the Badwater deposits.

Phenacolemur mcgrewi Robinson, 1968

Phenacolemur mcgrewi Robinson, 1968

Ignacius mcgrewi Bown and Rose, 1976

Holotype.—CM 15635, LM¹, locality 5 Front.

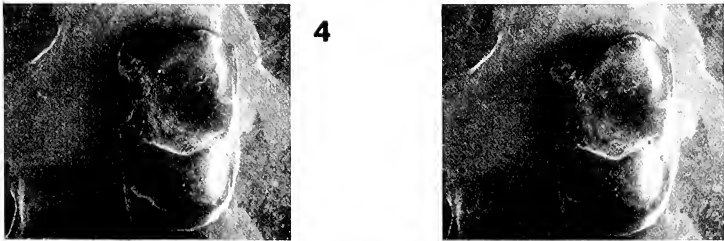
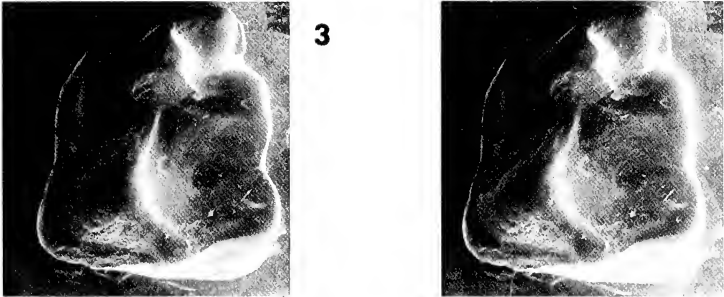
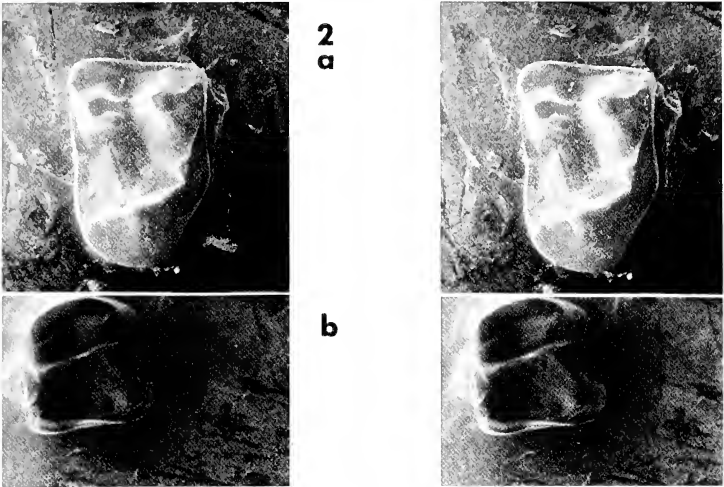


Fig. 2.—*Phenacolemur shifrae*, new species. (a) CM 15797, RM², holotype; (b) UCM 38323, RM₂; both approx. $\times 13$.
Fig. 3.—*Mytonius hopsoni*. CM 15068, LM₁; approx. $\times 9$.
Fig. 4.—*Chumashius* sp. CM 31275, RM¹; approx. $\times 9$.

Referred specimens.— M_2 : CM 29005, 15793, UCM 26012; M^1 : CM 15795, 15796; M^2 : CM 15794.

Localities.—5A, 5 Front, 6, 20; Badwater Creek area, Wyoming.

Known distribution.—Uintan and Duchesnean, Wyoming.

Emended diagnosis.—Known teeth (M^1 , M_2^2) smaller than those of *P. praecox*, *P. citatus*, *P. jepseni*, larger than those of *P. simonsi*, but close in size to those of *P. pagei*. M^{1-2} less quadrate, more transverse (lower L/W ratios) with shallower posterointernal basins than North American species of *Phenacolemur* except *P. pagei*; M^1 lacks the mesostyle, the deep ectoflexus and strong ectocingulum of the latter; M_2 narrower in proportion to length than that of *P. pagei* and lower crowned.

Description and remarks.—Of the specimens originally assigned by Robinson (1968) to *P. mcgrewi* only the type (M^1 , CM 15635) and an isolated M_2 (CM 26012) belong here. The smaller teeth he identified as second molars are referred below to a new species of *Phenacolemur*. New material of *P. mcgrewi* includes an M^2 , which, except for its slightly shorter length, bears the morphology of M^1 ; the paracone is larger than the metacone; the postprotocingulum (=protocone fold) and postcingulum enclose a shallow posterointernal basin; the conules are evident as thickenings on the pre- and postprotocristae, with the paraconule slightly stronger.

Among North American species of *Phenacolemur*, *P. mcgrewi* most closely resembles the Tiffanian *P. pagei* in known parts of the dentition. M^1 of the two species is virtually identical except for a tiny mesostyle, a broader ectocingulum and deeper ectoflexus in the latter. M^2 of *P. pagei* lacks a mesostyle, but the ectocingulum and ectoflexus are stronger than on that of *P. mcgrewi*.

***Phenacolemur shifrae*, new species**
(Fig. 2; Table 1)

Holotype.—CM 15797, RM^2 , locality 6, Badwater Creek area, Uintan, Wyoming.

Referred specimens.— M^1 : CM 15103, 15798; M^2 : CM 14598, 15799; M_2 : CM 21637, UCM 38323; M_3 : CM 15726.

Localities.—5, 5A, 6, Badwater Creek area, Wyoming.

Known distribution.—Uintan, Wyoming.

Diagnosis.—Smallest known species of *Phenacolemur*.

Etymology.—Named for Shifra Krishtalka.

Description and remarks.—*P. shifrae* is closest in size to the Wasatchian *P. simonsi*, but M^{1-2} of the former are significantly shorter anteroposteriorly and more transverse (L/W ratio lower) and have weaker protocristae and postcingula, a smaller, shallower posteroin-

ternal basin, and shorter protocone fold. In these features *P. shifrae* most closely resembles *P. mcgrewi* and the Tiffanian *P. pagei*, although M^{1-2} of *P. shifrae* are significantly smaller. M_{2-3} , the only known elements of the lower dentition in *P. shifrae*, are slightly shorter and narrower than that of *P. simonsi*, and M_3 has a narrower third lobe.

The extremely similar morphology of M^{1-2} of *P. mcgrewi*, *P. shifrae*, and *P. pagei* may imply that these three species are the most closely related among known species of *Phenacolemur*. Their disjunct temporal distribution—absence of these or closely related species from the Wasatchian or Bridgerian record—is not particularly disturbing and does not mitigate against their apparently close relationship. *Phenacolemur* was long thought to have become extinct in the early Eocene until it was recovered from the Badwater Uintan deposits. Some species may have occupied habitats during the Eocene that were far from areas of deposition that account for currently preserved and sampled deposits. This bias of facies is also reflected in the record of Eocene multituberculates, rodents, dermopterans, some insectivores, and artiodactyls (Black, 1967, 1978; Krishtalka and Black, 1975; Krishtalka and Setoguchi, 1977).

Family Anaptomorphidae

Trogolemur Matthew, 1909

Trogolemur sp.

Referred specimens.— M_1 : UCM 26043; dP_5 : CM 16019 (L, 1.8; PW, 1.3).

Localities.—5A, Wood.

Known distribution.—Uintan, Wyoming.

Remarks.—Robinson (1968) identified two isolated M_1 s, CM 15066 and UCM 26043, as *?Trogolemur* sp., an action corroborated by Szalay (1976) and this author. Unfortunately, one of these teeth, CM 15066, has since been lost. One diagnostic feature of P_5 and M_1 of *Trogolemur* is the posterior disposition of the metaconid and strong connection to the cristid obliqua. A Y-shaped groove separates the trigonid cusps on M_1 .

The dP_5 thought to belong here bears this characteristic morphology. The semimolariform trigonid on CM 16019 is laterally compressed, with the paracristid linking a distinct protoconid and a tiny anterior paraconid. The metaconid, taller than the protoconid, is isolated from the trigonid but is joined to a steep cristid obliqua. The talonid is fully molariform. In size and crown morphology, the M_1 closely resembles that of the Bridgerian *T. myodes*, but referral of the Badwater material to this species must await recovery of a larger sample.

Table 1.—*Dimensions of teeth of Phenacolemur mcgrewi and P. shifrae.*

Catalog no.	M ¹		M ²		M ₁		M ₂		M ₃	
	L	W	L	W	L	PW	L	PW	L	W
<i>Phenacolemur mcgrewi</i>										
CM 15635	2.0	2.8+								
CM 15795	2.0	—								
CM 15796	2.0	—								
CM 15794			1.8	2.9						
CM 29005					2.0	1.85				
CM 15793					2.0	1.8				
UCM 26012					2.0	—				
<i>Phenacolemur shifrae</i>										
CM 15103	1.4	2.0								
CM 15798	1.4	—								
CM 15797			1.3	2.0						
CM 14598			1.3	1.9						
CM 15799			1.2	1.9						
CM 21637							1.5	1.3		
UCM 38323							1.4	1.3		
CM 15726									1.9	1.1

Family Omomyidae

Type genus.—*Omomys* Leidy, 1869.

Included genera.—*Omomys*, *Chumashius*, *Macrotarsius*, *Tarsius*, *Pseudoloris*, *Uintanius*, *Tinimomys*, *Uintasorex*, *Niptomomys*, and, tentatively, *Mytonius* and *Ourayia*.

Known distribution.—Wasatchian to Chadronian, North America; Lutetian, Europe; Recent, Asia.

Emended diagnosis.—Tarsiiform primates (Fig. 1, node 3) with widely parabolic pre- and postprotocristae on M¹⁻³ that enclose a broad, shallow trigon basin; cristid obliqua on P₅M₁₋₃ originates buccal to the midline of the tooth so that the hypoflexid notch is shallow; entoconid and hypoconid flattened on lower molars.

Subfamily Omomyinae

Type genus.—*Omomys* Leidy, 1869.

Included genera.—*Omomys*, *Chumashius*, *Macrotarsius*, *Tarsius*, *Pseudoloris*, *Uintanius*, and, tentatively, *Ourayia* and *Mytonius*.

Known distribution.—Wasatchian to Chadronian, North America; Lutetian, Europe; Recent, Asia.

Emended diagnosis.—Omomyid primates (see above and Fig. 1, node 4) in which the paraconid and metaconid on M₁₋₃ are distinct and separate but are joined lingually by a weak crest. A morphocline

among members of this subfamily involves the progressively more anteromedial occurrence of the paraconid on M_{1-3} .

Ourayia Gazin, 1958

In the twenty years since *Ourayia* was named, it has had a mercurial taxonomic history. Gazin (1958) correctly separated *Ourayia uintensis* from Wortman's (1904) *Omomys*, with AMNH 1899, a partial right dentary with $P_4P_5M_1M_2$, from the Uintan (Uinta B) of Utah, as the type. Simons (1961) then allocated to *Ourayia* a mandibular fragment with M_1 (AMNH 1900, Uinta B, Utah), paired dentaries and associated palate (PU 16431, White River Pocket, Uinta B, Utah), and a second set of paired dentaries (PU 11236, Kennedy's Hole, Uinta B, Utah). Robinson (1968) disagreed with Simons and identified PU 16431 and PU 11236 as a new species of *Hemiacodon*, *H. jepseni*. At the same time he named a new genus and species, *Mytonius hopsoni*, from a partial right dentary with P_5-M_2 (YPM 15266) and an isolated M_2 (CM 12309), both from Myton Pocket, Uinta C, Utah. Szalay (1976), in the most recent review of *Ourayia*, concurred with Simons, reassigned PU 16431 and PU 11236 to *O. uintensis* and added YPM 15266 and CM 12309 to the species, thus synonymizing *H. jepseni* and *M. hopsoni* with *O. uintensis*. In these studies reconstructions of *Ourayia*'s relationships involved either *Hemiacodon*, *Omomys*, or *Macrotarsius*.

Except for Gazin's and Robinson's analysis, diagnostic criteria on the type of *Ourayia* have been overlooked. On AMNH 1899 P_4 is much taller than P_5 ; the P_5 paraconid is not a distinct cusp but forms the bulge-like anterior end of a strong paracristid; M_1 becomes much broader posteriorly and the cristid obliqua originates buccally, below the apex of the protoconid; M_2 , with a strong labial cingulid and anteroposteriorly compressed trigonid is more nearly square in occlusal outline than M_1 ; the buccal contour of M_{1-2} is not emarginate between talonid and trigonid; a distinct paraconid is not discernible on M_2 in the convex protoconid-metaconid crest that forms the leading edge of the trigonid, although one may have occurred on an unworn molar; the cristid obliqua on M_2 originates more labially from the posterior face of the protoconid than on M_1 , resulting in a shallower hypoflexid notch; on M_{1-2} the hypoconulid is merely a median flexure of the hypocristid.

Accordingly, comparison of PU 11236 with AMNH 1899 leaves no doubt that the paired partial dentaries from the Kennedy's Hole locality are referable to *Ourayia uintensis*. PU 11236 adds to our knowledge of *Ourayia* the nature of unworn M_2 , the morphology of M_3 and the alveoli anterior to P_4 . On M_{2-3} of PU 11236 a nubbin-like paraconid occurs close to the metaconid and is part of the arcuate protoconid-metaconid crest, so that the trigonid of these molars is closed lingually.

The absence of an M_2 paraconid on the type of *Ourayia*, AMNH 1899, is clearly due to wear. The hypoconulid lobe on M_3 of PU 11236 is short and the metaconid on M_{2-3} is reduced in comparison to M_1 .

Contrary to Robinson's (1968) conclusion, PU 11236 differs generically from *Hemiacodon*. Unlike *Ourayia* (AMNH 1899, 1900, PU 11236), M_{1-3} of *Hemiacodon* are significantly more angular in occlusal outline, especially along the buccal margin of the crown, and the talonid and trigonids cusps are higher. The cristid obliqua on M_{1-2} of *Hemiacodon* originates lingually from the posterolingual part of the base of the metaconid, resulting in a deeper hypoflexid notch, especially on M_2 . On M_2 of *Hemiacodon* the metaconid is not reduced and the trigonid is open lingually, because the paraconid is strong and separate from the metaconid. The hypoconulid lobe on M_3 of *Hemiacodon* is much longer.

The affinities of PU 16431, the palate and paired dentaries from White River Pocket, Utah, are likewise clear upon comparison to AMNH 1899 and PU 11236, type and referred material of *Ourayia*. Unlike *Ourayia*, on PU 16431 the P_4 is equal in height to P_5 , the paraconid is strong and separate on M_2 , the trigonid is not compressed, the paracristid is straight and the metaconid is not reduced. M_3 on PU 16431 is longer due to a well developed hypoconulid lobe. The features of P_5 and the lower molars that differentiate PU 16431 from *Ourayia* are shared with *Hemiacodon*. However, M_{1-3} of PU 16431 are equally distinct from *Hemiacodon* in occlusal outline (less angular, non-emarginate buccal contour, more nearly quadrate), position of the cristid obliqua (originates labially below protocone), and in having a shallow hypoflexid notch—features that PU 16431 shares with *Ourayia*. PU 16431 is distinct from both *Ourayia* and *Hemiacodon* in the structure of P_{4-5} —both premolars are shorter due to a shorter talonid and also on P_5 to a more triangular, molariform trigonid. The paraconid on P_5 is distinct cusp rather than part of a crest and occurs anterolingual rather than directly anterior to the protoconid. Additionally, the metaconid on M_{1-3} of PU 16431 is more bulbous and bears a sharp vertical crest, or cutting edge, on its posterior face. Upper molars of PU 16431 are even more distinct from those of *Hemiacodon*; they are more nearly quadrate (rather than transversely elongate), their posterior borders are not emarginate, their styler areas are larger and bear a mesostyle and separate anterior and posterior ectocingula. Comparison with *Ourayia* is not possible because the upper dentition of the latter is not known.

The associated upper and lower dentitions of PU 16431 are virtually identical to those of *Macrotarsius*. Indeed, features previously cited by Szalay (1976) and Robinson (1968) as diagnostic of *Macrotarsius* correspond to the ones listed above in distinguishing PU 16431 from

Ourayia and *Hemiacodon*. PU 16431 is referred below to a new species of *Macrotarsius*.

Identification of YPM 15266 and CM 12309, Robinson's (1968) type and referred specimens of *Mytonius hopsoni*, is more difficult, because a diagnostic part of M_2 on YPM 15266—the lingual half of the trigonid—is broken away and with it knowledge of the metaconid and paraconid. Thus Robinson's association of CM 12309, a complete M_2 , with YPM 15266 is not at all certain. Compared to *O. uintensis* (AMNH 1899, AMNH 1900, PU 11236) P_5 on YPM 15266 is shorter and broader, the metaconid is extremely weak and the cristid obliqua is medial rather than buccal. On M_1 the protoconid is more medial and the metaconid is more posterior than on M_1 of *Ourayia* resulting in a more oblique orientation of the posterior edge of the trigonid. YPM 15266 appears to be distinct from *O. uintensis*, whereas CM 12309 is not. Until more complete material is recovered it seems prudent to retain YPM 15266 as the type of *Mytonius hopsoni* rather than an extreme variant of *Ourayia*. Other material from Badwater and the Chadronian of South Dakota are also referable to *M. hopsoni*, as described below.

***Ourayia uintensis* (Osborn, 1895)**

Microsyops uintensis Osborn, 1895

?“*Microsyops*” *uintensis* Osborn, 1902

Omomys uintensis Wortman, 1904

Ourayia uintensis (Osborn, 1895) Gazin, 1958

Ourayia uintensis (Osborn, 1895) Simons, 1961, in part

Hemiacodon jepseni Robinson, 1968, in part

Mytonius hopsoni Robinson, 1968, in part

Ourayia uintensis (Osborn, 1895) Szalay, 1976, in part

Holotype.—AMNH 1899, partial right dentary with $P_{4-5}M_{1-2}$, from White River Pocket, Uinta B, Utah.

Referred specimens.—AMNH 1900, PU 11236, CM 12309.

Localities.—Kennedy's Hole, White River Pocket and Myton Pocket, Uinta Formation, Utah.

Known distribution.—Uintan, Utah.

Emended diagnosis.— P_4 higher than P_5 ; P_5 trigonid with anterior, bulge-like paraconid and discrete metaconid, talonid short with buccal cristid obliqua; cristid obliqua on lower molars originates buccally on posterior face of protoconid; M_2 paraconid tiny nubbin on arcuate protoconid-metaconid cristid; buccal border of lower molars not emarginate; talonid much broader than trigonid on M_1 ; M_2 quadrate with low, flat talonid cusps; hypoconulid lobe on M_3 short.

Discussion.—*O. uintensis* is the only known species of the genus. Without knowledge of its upper dentition, any conclusions concerning the relationships of *Ourayia* are tentative. Based on the lower dentition

alone, *Ourayia* appears to be an omomyid and most closely related to *Macrotarsius*. M_{1-2} of *Ourayia* and *Macrotarsius* are derived in their quadrate occlusal outline, non-emarginate buccal contour and in the extreme buccal position of the cristid obliqua.

The alveoli anterior to P_4 are well preserved on the partial right dentary of PU 11236. The crown of the anteriormost tooth is broken away, but the base is large, laterally compressed and caniniform, and, as in all Plesitarsiiformes, is identified as a canine (Schwartz and Krishtalka, 1976, 1977; Schwartz, in press; Krishtalka and Schwartz, manuscript). The shape and position of the three alveoli between C_1 and P_4 imply that these bore single-rooted teeth, here dubbed $dP_1P_2dP_3$. Whether the first and third premolars were retained deciduous teeth is not certain. The alveolus for dP_1 is rectangular and compressed anteroposteriorly, whereas that for P_2 is much larger and oval. The dP_3 alveolus, also oval, is smaller than that for P_2 but slightly larger than that for dP_1 . This pattern of alveolar size— P_2 larger than dP_1 or dP_3 —is common among plesitarsiiforms that have these teeth.

Mytonius Robinson, 1968

Mytonius hopsoni Robinson, 1968

(Fig. 3; Table 2)

?*Hemicodon* sp. Robinson, 1968

Mytonius hopsoni Robinson, 1968, in part

Ourayia uintensis Szalay, 1976, in part

Macrotarsius? sp. Szalay, 1976

Holotype.—YPM 15266, partial right dentary with P_5 – M_2 , from Myton Pocket, Uinta Formation (Uinta C), Uintan of Utah.

Referred specimens.— M_1 : CM 15068; partial right dentary with P_5 – M_1 : CM 10855.

Localities.—5A, Badwater Creek area, Wyoming (CM 15068); Short Pine Hills, South Dakota (CM 10855).

Known distribution.—Uintan, Utah and Wyoming; Chadronian, South Dakota.

Emended diagnosis.— P_5 shorter and broader than *Ourayia*, with complete buccal cingulid and more medial cristid obliqua; metaconid weak on posterolingual face of protoconid. P_5 trigonid more premolariform than in *Macrotarsius*. M_1 trigonid more laterally compressed, with a more medial protoconid and posterior metaconid than in *Ourayia* and *Macrotarsius*.

Remarks.—The three specimens referred here seem, at least tentatively, to represent a single species. As noted in other sections, CM 15068 from Badwater does not resemble M_1 of *Hemicodon* (Robinson, 1968) and certainly not M_1 of *Macrotarsius* (Szalay, 1976). CM 10855 also differs significantly from P_5 – M_1 of *Macrotarsius* and strict definition of *Ourayia* (pace Szalay, 1976) excludes YPM 15266.

Chumashius Stock, 1933**Chumashius sp.**

(Fig. 4)

Referred specimens.— M_1 : CM 15069; M^1 : CM 31275, 28827; M^3 : CM 16011, 28641.

Localities.—5A, Wood, Badwater Creek area, Wyoming.

Known distribution.—Uintan, Wyoming.

Remarks.—Robinson (1968) correctly identified an isolated M_1 (CM 15069) as ?*Chumashius* sp.—a record omitted by Szalay (1976) in his review of the genus. Four more isolated teeth—two partial M 's and two M^3 s—also closely resemble *Chumashius*, but the material is too poor to be assigned confidently to *C. balchi*.

Like *Omomys*, *Macrotarsius*, and other tarsiiforms (Fig. 1, node 3) upper molars of *Chumashius* bear the derived widely divergent or parabolic protocristae that enclose a broad, shallow trigon basin. *Chumashius* is an omomyine in that the paraconid on the lower molars occurs medially rather than lingually. In both *Chumashius* and *Pseudoloris* the paraconid is closer to the protoconid than the metaconid on M_{1-3} .

Macrotarsius Clark, 1941

Three species of *Macrotarsius* are recognized here—the type species, *M. montanus*; *M. siegerti*, from Badwater, and a new species, *M. jepseni*, from the Uintan of Utah. *M. montanus* (Clark, 1941) is known only from the type, CM 9592, a partial right dentary with P_3 , P_5 – M_3 . Robinson (1968) and Szalay (1976) list difference in size as the lone diagnostic criterion distinguishing *M. siegerti* from *M. montanus*. Although comparable teeth of *M. montanus* are consistently slightly longer or wider than those in the sample of *M. siegerti*, statistically, the difference in size is on the order of intraspecific variation. Known parts of the dentition differ significantly only in crown shape; P_5 – M_3 of *M. montanus* are more bulbous (exodaenodont) labially.

Macrotarsius siegerti Robinson, 1968

(Figs. 5, 6, 7; Tables 2, 3)

Holotype.—CM 15122, RP_5 , locality 5A, Badwater Creek area, Uintan, Wyoming.

Referred specimens.— P_4 – P_5 : CM 15800; P_5 – M_1 : CM 21990; P_5 : UCM 26009; M_1 : CM 16063, 16809, 15072, 28825; M_2 : CM 15147; M_3 : CM 14601, 15674, 19761; P^5 – M^3 : CM 18646; M^{1-3} : CM 14549, 15056; M^{2-3} : CM 15052; P^5 : (tentatively) CM 15610, 15717; M^3 : CM 28826.

Localities.—5, 5A, 5 Front, 5 Back, 6, Wood.

Known distribution.—Uintan, Wyoming.

Description and remarks.—The morphology of the known parts of

Table 2.—Dimensions of lower teeth of *Macrotarsius montanus*, *M. siegerti*, *M. jepseni*, *Ourayia uintensis*, and *Mytonius hopsoni*.

Taxa and no. of specimens	P ₃			M ₁			M ₂			M ₃		
	L	W		L	PW		L	PW		L	PW	
<i>Macrotarsius montanus</i>	3.2	3.2		4.6	4.1		4.6	4.0		5.7	3.7	
N	1	1		1	1		1	1		1	1	
<i>Macrotarsius siegerti</i>	3.2-3.4	2.8-2.9		4.0-4.6	3.4-3.7		4.4	3.6		4.9-5.2	3.3-3.3	
N	4	4		4	4		1	1		2	3	
<i>Macrotarsius jepseni</i>	2.9-3.0	2.5		4.0	3.4		4.1	3.5-3.6		5.0	3.1	
N	2	2		1	1		2	2		1	1	
<i>Ourayia uintensis</i>	3.5-3.6	2.4-2.5		4.1-4.3	3.1-3.5		3.9-4.0	3.4-3.7		4.5	3.0-3.1	
N	3	3		2	3		3	3		2	2	
<i>Mytonius hopsoni</i>	2.7-3.0	2.4-2.7		3.5-3.8	3.0-3.1		3.5	3.5		—	—	
N	2	2		3	2		1	1		—	—	

Table 3.—Dimensions of upper teeth of *Macrotarsius siegerti* and *M. jepseni*.

Taxa and no. of specimens	P ₃			M ₁			M ₂			M ₃		
	L	W		L	W		L	W		L	W	
<i>Macrotarsius siegerti</i>	2.9-3.2	3.8-4.6		4.0-4.2	5.1-5.2		4.0-4.2	5.3-5.4		3.0-3.7	4.8-5.2	
N	3	3		3	4		4	3		3	4	
<i>M. jepseni</i>	2.9	3.8		3.8	4.8		3.9	5.1		3.4-3.5	4.6-4.7	
N	2	2		2	2		2	2		2	2	

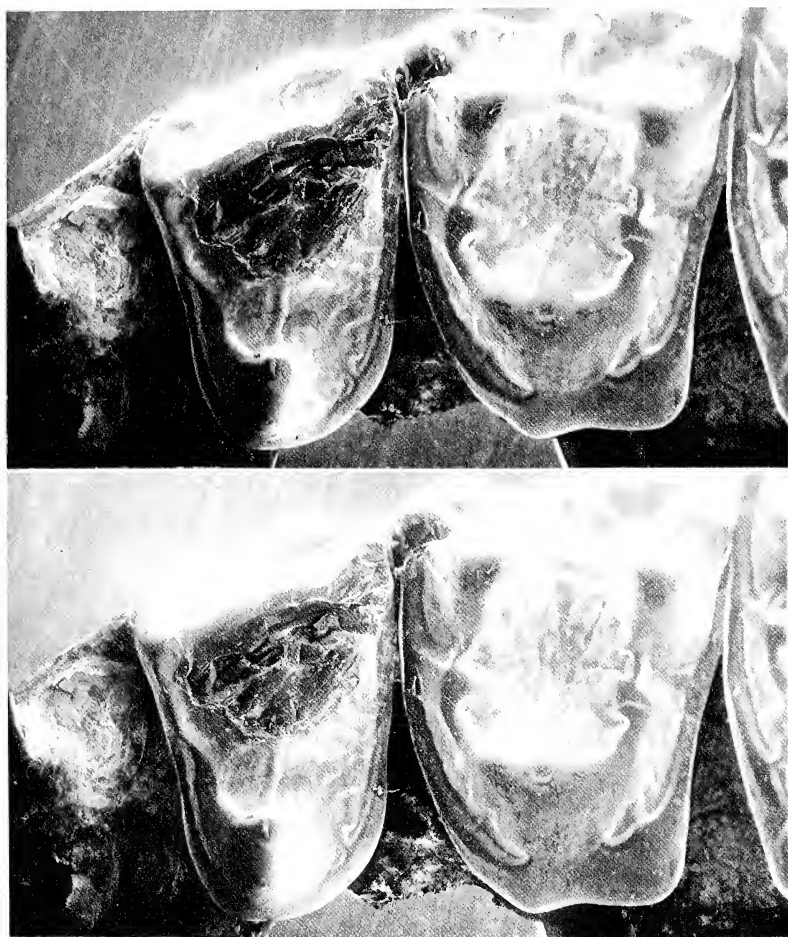


Fig. 5.—*Macrotarsius siegerti*. CM 18646 (part), LP⁵-M¹; approx. $\times 11$.

the lower dentition of *Macrotarsius* was adequately described by Clark (1941), Robinson (1968), and Szalay (1976). Four additional aspects, however, deserve comment.

(1) A recently recovered specimen of *M. siegerti*, CM 15800, preserves a number of premolars and the anterior part of the dentary including the symphyseal area and all alveoli. The shape and position of these alveoli are identical to those on CM 9592, type of *M. montanus*. The first alveolus, extremely large and laterally compressed, opens anterodorsally and on CM 9592 contains an enlarged tooth that

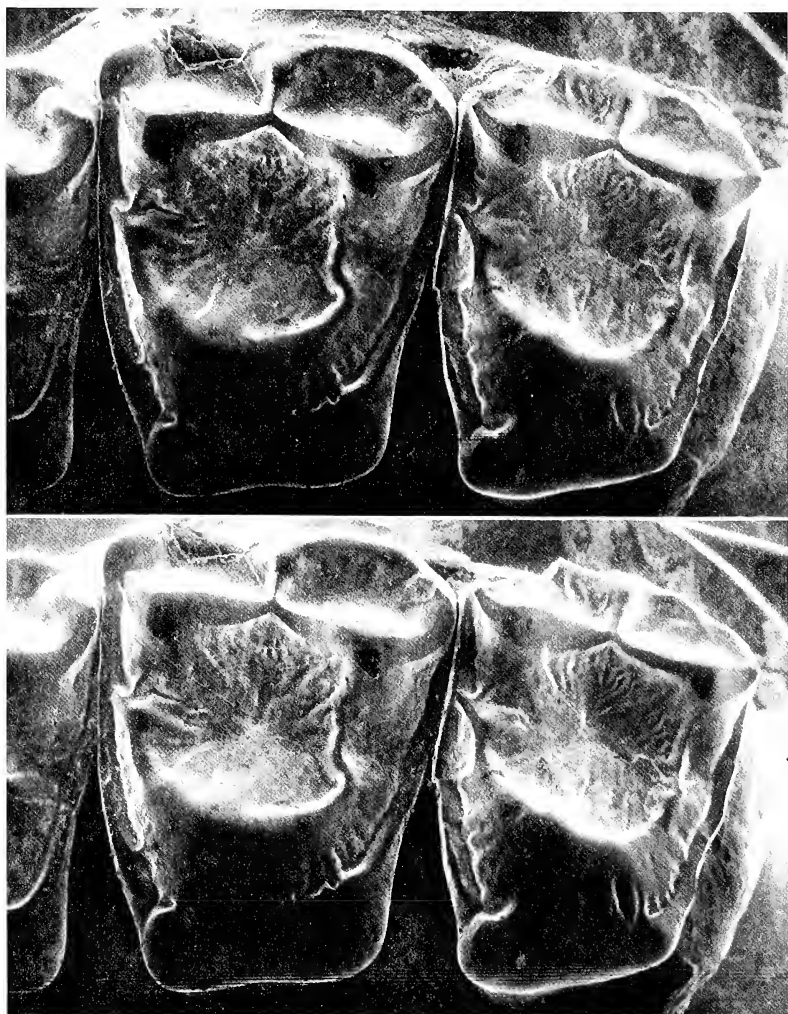


Fig. 6.—*Macrotarsius siegerti*. CM 18646 (part), LM²⁻³; approx. $\times 11$.

typically is the anteriormost, usually caniniform, tooth in known pleiadapiform-tarsiiform primates (Schwartz and Krishtalka, 1976, 1977). The next alveolus is tiny and contained a single-rooted tooth. The following alveolus is larger, oval, and in CM 9592, is occupied by a worn, single-rooted premolar. Behind this tooth is an alveolus for another single-rooted tooth, followed by two double-rooted premolars. The suggested lower antemolar dental complement of *M. siegerti* and

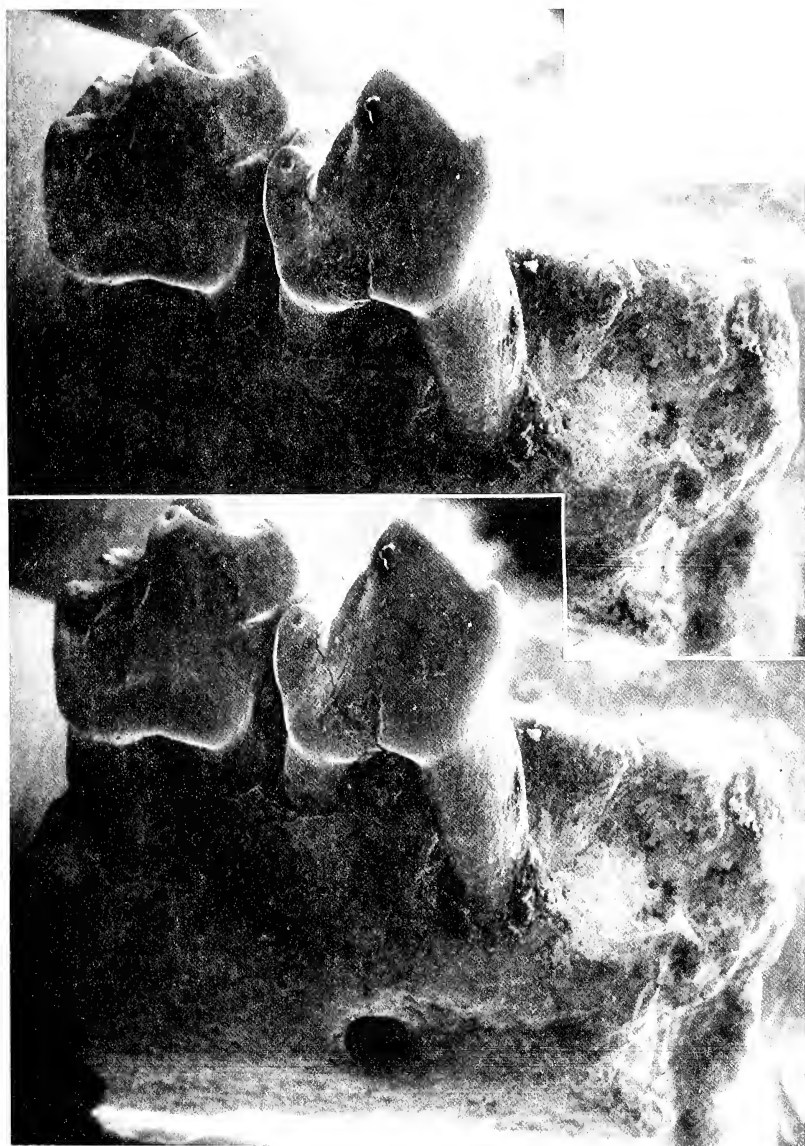


Fig. 7.—*Macrotarsius siegeri*. CM 15800, partial right dentary with P₄₋₅ and alveoli for C, dP₁, P₂, dP₃; approx. $\times 12$.

M. montanus is a canine and five premolars or, more specifically, CdP₁P₂dP₃P₄P₅.

(2) Two significant features were omitted by Szalay (1976) from his comparison of *Macrotarsius* and *Ourayia*—in *Macrotarsius*, a more molariform trigonid on P₅ and a separate paraconid and open trigonid on M₂. The paraconid on P₅ of *Ourayia* occurs nearly directly anterior to the protoconid, with a high cristid linking the two cusps; the P₅ paraconid of *Macrotarsius* is closer to the metaconid and anterolingual to the protoconid so that the three cusps form a V-shaped trigonid. P₄, broken on CM 9592, but complete on CM 15800, is lower and similarly more molariform than that of *Ourayia*. The trigonid, longer and narrower than the talonid, bears a low protoconid, a small paraconid, and a strong cristid on the posterior face of the protoconid. P₄ of *Ourayia* is longer and narrower than that of *Macrotarsius*, bears a higher protoconid and lacks a paraconid.

(3) CM 15068 (L, 3.7; PW, 3.0), a left M₁, was identified as ?*Hemicodon* sp. by Robinson (1968) and as *M. siegerti* by Szalay (1976), but falls well below the range in size of M₁ of *M. siegerti* (Szalay, 1976:288, Table 18). M₁ of *Macrotarsius* characteristically has a lingually bulbous metaconid and hypoconid, a vertical cristid (=cutting edge of Szalay, 1976) along the posterior face of the metaconid and lacks a labial cingulid. In contrast to *Macrotarsius* but like *Ourayia* and *Mytonius*, the lingual face of the crown is not bulbous on CM 15068, the cristid on the posterior face of the metaconid is absent, and a cingulid occurs along the labial contour of the crown. CM 15068 resembles *Mytonius* and differs from *Ourayia* in its more laterally compressed trigonid—the protoconid is more medial and the metaconid more posterior.

(4) Szalay (1976:287, Fig. 78) alluded to a Chadronian record of ?*Macrotarsius* sp. from CM 10855, a partial right dentary with P₅ and a broken M₁ from the Short Pine Hills, South Dakota, although neither the specimen nor the taxon is mentioned in text. P₅ on CM 10855 is more premolariform (weak metaconid, no distinct paraconid) than that of *Macrotarsius*, much shorter and wider and with a lower protoconid than that of *Ourayia*, but is most similar to that of *Mytonius hopsoni* (YPM 15266) as is the preserved remnant of M₁.

Upper teeth known in *M. siegerti* are P⁵–M³ and these, especially M³, exhibit a noteworthy range of variation. P⁵ is triangular and transverse in occlusal view, with a well-developed postcingulum and a parastylar ectocingulum. Unfortunately, much of P⁵ is broken away on CM 18646 [*pace* Szalay's illustration (1976:291, Fig. 81) of a complete P⁵, which, although not noted as such, is a reconstruction]. Two isolated P⁵s (CM 15717 and CM 15610) identified as *Macrotarsius* by Robinson (1968) and Szalay (1976) are less transverse than P⁵ on CM

18646 and lack the ectocingula on the latter. These are tentatively retained in *M. siegerti*.

M^{1-3} of *M. siegerti*, though quadrate in occlusal outline, are wider than long and longer labially than lingually. Paracone and metacone are robust and pyramidal with strong cristae. The protocone is broad and bears strong pre- and postprotocristae that form a parabola enclosing a broad trigon basin. A mesostyle, at the anterior end of a metastylar ectocingulum, is joined by a crest to the medial apex of the centrocrista. A parastylar ectocingulum, weaker than its metastylar counterpart, does not make contact with the mesostyle. The conules are poorly developed, with the paraconule slightly larger. The pre- and postcingula are strong and terminate lingually in a tiny pericone and hypocone, respectively. The degree of development of the ectocingula, mesostyle, pericone and hypocone varies considerably from CM 18646 (strong) to CM 14549 (extremely weak); the remainder of the hypodigm is intermediate in the expression of these characters. M^3 on CM 14549 is more nearly triangular than quadrate, because the posterolingual corner of the crown is not expanded posteriorly.

Macrotarsius jepseni (Robinson, 1968)

Ourayia uintensis Simons, 1961, in part

Hemicacodon jepseni Robinson, 1968, in part

Ourayia uintensis Szalay, 1976, in part

Holotype.—PU 16431, palate with upper dentition except left P^2 , paired partial dentaries with left C, P_{4-5} , M_{1-3} and right C, P_4 , M_{1-3} ; from White River Pocket, Uinta Formation, Utah.

Known distribution.—Uintan, Utah.

Diagnosis.—Compared to *M. siegerti*, mesostyle on M^{1-3} small, not connected to centrocrista; P^5 less transverse. Compared to *M. siegerti* and *M. montanus*, P_1 alveolus unreduced, P_{1-3} alveoli more widely spaced, diastema between P_3 alveolus and P_4 , $P_{4-5}M_{1-3}$ not exodaenodont buccally.

Description and remarks.—Unlike *M. siegerti*, the mesostyle on M^{1-3} of *M. jepseni* is not linked to the median flexure of the centrocrista. Otherwise the upper molars of both species are identical in crown morphology. As in *M. siegerti* and *M. montanus* the alveolus for P_2 in *M. jepseni* is larger than that for P_3 and the latter is larger than that for P_1 . However in the two former species the P_1 alveolus is tiny and lingually displaced, the P_{1-3} alveoli are crowded and adjacent antero-posteriorly, and there is no diastema between the alveoli for P_3 and the anterior root of P_4 . In contrast, the P_1 alveolus in *M. jepseni* is oval and unreduced, the alveoli for P_{1-3} do not border one on the other and a distinct diastema occurs between P_3 alveolus and P_4 . Although the length along the dentary from the symphyseal border to the pos-

terior tip of M_3 is equal in *M. jepseni* and *M. montanus*, the posterior premolars and molars of the latter are larger—a condition made possible by the inferred crowding of the anterior premolars and reduction of P_1 . $P_{4-5}M_{1-3}$ of *M. montanus* and *M. siegerti* are also broader than those of *M. jepseni* due to the buccal exodaenodontology of these teeth.

Apart from these differences, which in total imply specific distinction for this material from Utah, PU 16431 exhibits the shared-derived features of *Macrotarsius*—molariform trigonid on P_5 ; broad, quadrate molars with a mesostyle on a posterior ectocingulum on M^{1-3} ; a vertical crest on the posterior face of the metaconid on M_{1-3} . *M. montanus* and *M. siegerti* are derived with respect to *M. jepseni* in the crowding of the anterior lower premolars, the extreme reduction and lingual displacement of the P_1 alveolus, the buccal exodaenodontology of $P_{4-5}M_{1-3}$, and the connection of the mesostyle to the centrocrista on M^{1-3} (known only in *M. siegerti*).

PU 16431 adds the morphology of the lower canine and teeth anterior to P^5 to our knowledge of *Macrotarsius*. The crown of the lower and upper canine is semispatulate, without digitations and, on the former, has a raised internal margocristid (Gingerich, 1976). P^1 is a trenchant, laterally compressed blade that is almost as large as the upper canine. Its large single root appears to be the result of fusion of two roots. P^2 and P^3 are subequal, single-rooted, smaller than P^1 but, like the latter, are trenchant blades with a tiny posterobasal cuspule. P^4 , triangular in occlusal view, is narrower than P^5 and bears a high paracone that occupies most of the crown and a small lingual protocone.

On PU 16431 a premolariform tooth is glued to the anterior root of P_4 that forms the anterior edge of the specimen. The association of this alleged P_3 with PU 16431 is highly questionable; the alveolus for RP_3 is not preserved and the tooth is black, whereas all the teeth that are undoubtedly part of PU 16431 are brown.

Subfamily Uintasoricinae

Uintasoricinae Szalay, 1969b.

Uintasoricinae Bown and Rose, 1976, in part.

Type genus.—*Uintasorex* Matthew, 1909

Included genera.—*Uintasorex*, *Tinimomys*, *Niptomomys*.

Known distribution.—Wasatchian to Uintan, North America.

Emended diagnosis.—Tiny omomyids with enlarged P_5^5 , semimolariform P_5 , absence of premolars at P_1 and P_3 loci, paraconid reduced or absent on M_{2-3} .

Remarks.—*Uintasorex*, *Niptomomys*, and *Tinimomys* share the omomyid tarsiiform condition (Fig. 1, node 3) of parabolic protocristae on the upper molars that demarcate a broad, shallow trigon basin. The

crisid obliqua on the lower molars originates labially, below the protoconid, so that the hypoflexid notch is shallow. As omomyids, these three genera constitute the Uintasoricinae and are most closely related to their sister group, the Omomyinae.

Identification of uintasoricines as tarsiiforms is contrary to recent discussions of their affinities (Szalay, 1969b; Bown and Gingerich, 1972, 1973; Bown and Rose, 1976), although McKenna (1960) recognized the similarities between *Niptomomys* and omomyids. Szalay (1969b) erected the Uintasoricinae for *Uintasorex* and *Niptomomys* and included the subfamily in the Microsyopidae. Earlier, Szalay (1969a) had tentatively referred the microsyopids to Primates, included the North American genera *Microsyops*, *Craseops*, and *Navajovius* (tentatively) in the family and considered *Cynodontomys* a junior synonym of *Microsyops*.

Among the diagnostic criteria of *Microsyops* are on M^{1-2} a hypocone at the lingual end of a postcingulum and lack of a protocone fold (=postprotocingulum of Bown and Gingerich, 1973) and on M_{1-3} a deep notch between the proximal and unreduced hypoconulid and entoconid.

At this time the Paromomyidae included, among others, the Paleocene genera *Plesiolestes*, *Palaechthon*, *Palenochtha*, and *Torrejonia*. These are characterized in part by absence of a hypocone, presence of a protocone fold that is continuous with the postcingulum on M^{1-2} , and a crest between the hypoconulid and entoconid.

As primates or non-primates [Szalay (1975, 1976) has since reversed his opinion] the microsyopids are accorded primitive status on the basis of an entotympanic bulla and medial entocarotid artery in *Microsyops* (Szalay, 1969a). If the microsyopids were primitive Eocene primates, where did their ancestry lie? Bown and Gingerich (1973) suggested that a *Plesiolestes* (Paleocene)-*Cynodontomys* (Eocene) lineage provided the answer, after detailed comparisons of the dentitions of the two genera. One apparent inconsistency is their unexplained recognition of both *Cynodontomys* and *Microsyops* subsequent to Szalay's synonymy of the two genera. A second is the necessary loss of the protocone fold and hypoconulid-entoconid crest and appearance of a hypocone and a notch between a twinned hypoconulid and entoconid in the *Plesiolestes*-*Cynodontomys* transition—two important alleged evolutionary events that Bown and Gingerich (1973) say, but do not demonstrate, are functionally related.

In the same issue of that journal Szalay (1973) described a new Paleocene paromomyid (*Micromomys*), a new species of *Plesiolestes* (*P. sirokyi*) and synonymized *Torrejonia* (Gazin, 1968) with *Plesiolestes*. Most recently, Bown and Rose (1976) reclassified the Microsyopidae to include the four above mentioned paromomyids (*Plesi-*

olestes, *Palaechthon*, *Palenochtha*, *Torrejonia*) in the Microsyopinae and outlined the inferred relationships between microsyopines and uintasoricines. Here *Cynodontomys* is considered a junior synonym of *Microsyops* and *Torrejonia* is listed as a valid genus without mention of Szalay's relegation of that taxon to *Plesiolestes*. Their diagnosis of the Microsyopinae (including, among others, *Microsyops*, *Plesiolestes*, *Palaechthon*, *Palenochtha*, and *Torrejonia*) lists the notch between the hypoconulid and entoconid—a feature absent from M_{1-2} of the four latter genera. They regard *Plesiolestes* and *Palaechthon* ancestral to *Microsyops* and *Craseops*, whereas *Palenochtha* is considered basal to the uintasoricine microsyopids. This phylogenetic scheme would require parallel loss of the protocone fold and hypoconulid-entoconid crest and parallel appearance of a hypocone, twinned hypoconulid-entoconid, and a notch between the latter in the evolution of the two subfamilies of microsyopids—not an impossible occurrence, but perhaps not the most cogent interpretation of the dental evidence.

Apart from these difficulties, the suggestions of a close relationship among some paromomyids, uintasoricines, and microsyopines are not based on shared-derived characters but on an amalgam of primitive features and stratigraphic occurrences. All tarsiiforms, including uintasoricines (Fig. 1, node 3) have parabolic protocristae on M^{1-3} . All plesiadapiforms, including paromomyids (Fig. 1, node 5), have a protocone fold on M^{1-2} . Microsyopids (*Microsyops*, *Craseops*, *Navajovius*, *Alsaticopithecus*) lack these derived features and are not closely related to uintasoricines or paromomyids. Furthermore, the hypoconulid and entoconid in uintasoricines are not “twinned” in the sense that they are in microsyopids, marsupials, bats, or nyctitheriids. Because the hypoconulid in uintasoricines is a low, elongate thickening on the hypocristid, its lingual tip occurs near the entoconid. The supposed twinning is an artefact of the compression and lingual elongation of the hypoconulid.

Uintasorex Matthew, 1909

Uintasorex sp. cf. *U. parvulus* Matthew, 1909

No additional teeth of *Uintasorex* have been recovered since Robinson (1968) recorded the occurrence of this primate at Badwater. Like *U. parvulus*, but unlike the Uintan *U. montezumicus* (Lillegraven, 1976) the isolated upper molars have weak posterior cingula that lack a hypocone.

SUMMARY AND CONCLUSIONS

Seven species of primates are recorded from the late Eocene Badwater deposits: *Phenacolemur mcgrewi*; *P. shifrae* (Paromomyidae);

Chumashius sp.; *Macrotarsius siegerti*; *Mytonius hopsoni* (Omomyinae); *Uintasorex* sp. cf. *U. parvulus* (Uintasoricinae); *Trogolemur* sp. (Anaptomorphidae). The occurrence of late Eocene *Phenacolemur*, multituberculates, a high proportion of eomyid rodents, a dermopter-an, certain insectivores, and selenodont artiodactyls (Krishtalka and Black, 1975; Krishtalka and Setoguchi, 1977; Black, 1978; M. R. Dawson, personal communication) implies that certain levels in the Badwater sediments preserve a unique Uintan-Duchesnean facies—not the lowland, intermontane basin situation of most Eocene localities but, predominantly, a drier, upland, savannah woodland environment with restricted pockets of riverine, forested habitat.

Among the taxa discussed in this paper, *Phenacolemur* and *Ignacius* are provisionally maintained as separate genera, although *I. mcgrewi* is referred to *Phenacolemur*. *Ourayia* is not known from the upper dentition but includes only the holotype and associated partial dentaries from the Uintan of Utah. The palate and associated dentaries formerly assigned to *Ourayia* (Simons, 1961; Szalay, 1976) and *Hemiaco-don* (Robinson, 1968) are indistinguishable from *Macrotarsius* and comprise the type of *M. jepseni* from the Uintan of Utah. *Mytonius hopsoni* is tentatively recognized because the referred material, although sparse and fragmentary, differs significantly from the known sample of *Ourayia*.

New hypotheses of relationships among and generic composition of the major groups of plesiadapiform-tarsiiform primates are depicted in Fig. 1 and defined by inferred shared-derived characters. If these are correct, the Anaptomorphidae and Omomyidae as most recently reviewed by Szalay (1976) are unnatural groups. Contrary to Szalay's (1976:277, 280) conclusion, absence of a protocone fold on upper molars of "*Ourayia*" (= *Macrotarsius jepseni*) is not a specialization among omomyids, but a retained primitive condition of all tarsiiforms. The presence of a protocone fold among some plesitarsiiforms is one of the derived characters that implies their common ancestry—a relationship expressed taxonomically by the clade Plesiadapiformes (Fig. 1, node 5). Accordingly, this clade includes not only plesiadapids, carpolestids, and paromomyids (Gingerich, 1976) but also anaptomorphids and microchoerids (revised; see Fig. 1 for included genera). Cladistically, the Plesiadapiformes is a sister group of the Tarsiiformes, which only include omomyids (Omomyines and uintasoricines; revised, see Fig. 1 for included genera). They lack a protocone fold, but the protocristae on the upper molars are much more divergent and form a broad parabola enclosing a larger trigon basin (Fig. 1, node 3).

Accordingly, among the taxa discussed here, *Macrotarsius*, *Omo-mys*, *Chumashius*, and *Uintasorex* are tarsiiforms. *Ourayia* and *My-tonius*, known only from the lower dentition, are tentatively included

in the Omomyidae on the basis of derived features on P_5 - M_2 shared with *Macrotarsius*. *Hemiacodon*, with a strong protocone fold on M^{1-2} , is not an omomyid (*pace* Szalay, 1976), but, along with *Washakius*, *Shoshonius*, and *Loveina*, is a member of the Washakiinae, a subfamily of Anaptomorphidae (Fig. 1, nodes 7, 7B). On M^{1-2} of these four genera the postprotocrista is short, the pre- and postcingular end lingually in a pericone and hypocone, respectively, and the protocone fold-postcingulum junction is weak but marked by a tiny cuspsule or wear facet.

A more detailed synthesis of the relationships among described plesiadapiform-tarsiiform genera will appear elsewhere (Krishtalka and Schwartz, manuscript), along with a discussion of omitted taxa and synonymies.

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TAXONOMIC AND KARYOLOGIC COMMENTS ON SMALL BROWN BATS, GENUS *EPTESICUS*, FROM SOUTH AMERICA

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ABSTRACT

The South American species, *Eptesicus brasiliensis* (Desmarest), *E. furinalis* (D'Orbigny), and *E. diminutus* Osgood, were investigated in order to identify a collection of *Eptesicus* from Tucumán and Catamarca provinces, Argentina. The name *E. dorianus* (Dobson) cannot be applied to any of the known taxa, and is treated as a *nomen dubium*. All three species appear to be strongly dimorphic in size, with females being larger than males. The three species form a size continuum, with *E. diminutus* being the smallest species and *E. brasiliensis* being the largest. Some size overlap occurs between *E. furinalis* and the other species, but this usually involves males of the larger species and females of the smaller species. This size overlap has given rise to the misidentification of some specimens by previous workers, and has resulted in the mischaracterization of *E. diminutus*. Samples of a population of *E. furinalis* from Tucumán Province and adjacent areas in northwestern Argentina are larger than other known populations, and also differ in other details. This population is named as a new subspecies. The karyotypes of *E. furinalis* and *E. diminutus* are identical in appearance, and exhibit the same structure as other New World *Eptesicus*. The 50 chromosomes consist of 24 pairs of acrocentric autosomes, grading from large to small, a large submetacentric X chromosome, and a small acrocentric Y chromosome.

INTRODUCTION

The genus *Eptesicus* is represented in South America by seven species (Davis, 1966). A group of long-haired forms consists of *E. fuscus* (Palisot de Beauvois), *E. andinus* (J. A. Allen), and *E. montosus*

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Thomas. These species are primarily distributed along the Andes of northern South America, and in the lowlands of Colombia and Venezuela, except for *E. montosus*, which occurs from the highlands of Bolivia to the Planalto of southeastern Brazil. A group of short-haired species is represented by *E. innoxius* (Gervais), which occurs along the Pacific Coast in Ecuador and Peru, and by three wide-ranging species from the lowlands east of the Andes (Davis, 1966).

The three eastern species, *E. brasiliensis* (Desmarest), *E. furinalis* (D'Orbigny), and *E. diminutus* Osgood, are apparently sympatric in the Rio Paraná lowlands, along the coast from Maranhão, Brazil, to Buenos Aires, Argentina, and, perhaps, in the vast Caatinga, Serrado, and Chaco regions south of the Amazonian lowlands. The members of this sympatric assemblage are segregated by size, with *E. brasiliensis* being the largest and *E. diminutus* being the smallest. There appears to be some size overlap between species pairs, which has led to considerable confusion concerning the applicable names for certain populations, and the identity of individual bats. Furthermore, there are only a relatively few specimens, from widely scattered localities, of most taxa. Consequently, little is known about individual and secondary sexual variation, and most taxa are poorly characterized.

Early in this study it was discovered that the holotype of *E. dorianus* (Dobson) was much too large to be conspecific with the smallest species of South American *Eptesicus* (*E. dorianus* of Davis, 1966). Other available names for these bats are *E. diminutus* Osgood, 1915, and *E. fidelis* Thomas, 1920. Davis (1966) considered *E. fidelis* as a junior synonym of *E. dorianus*, and regarded *E. diminutus* as conspecific with *E. dorianus*, but recognizable as a subspecies. I also regard *E. diminutus* and *E. fidelis* as being conspecific, and because *E. diminutus* has priority, this name is used to refer to the smallest short-haired South American species of *Eptesicus*.

During the summer of December 1975 and January 1976, I collected and karyotyped specimens of *Eptesicus* from Aguas Chiquitas, a small stream at the southern end of the Sierra de Medina (approximately 800 m), about 4 km E of El Cadillal Dam, Tucumán Province, Argentina. In the process of identifying these specimens, and a specimen from Potrero Dike, El Potrero, Catamarca Province, Argentina, which together span the known size range from *E. diminutus* to *E. brasiliensis*, I have reviewed aspects of the variation and taxonomy of these *Eptesicus* species.

METHODS

The morphometric traits utilized in this study, their abbreviations, and, where necessary, explanations of the methods of measuring are listed below.

Cranial breadth (CB).—Greatest width of cranium immediately posterior to zygomatic arches.

Length of ear (EL).

Length of forearm (FAL).—Length of forearm, including wrist bones.

Length of fur (FL).—Length of pelage in interscapular region.

Greatest length of skull (GSL).—Distance from anteriormost point on incisors to posteriormost point of cranium.

Length of head and body (HBL).

Length of hind foot (HFL).—Length of hind foot, including claws.

Length of metacarpal 3 (M-III).—Length of metacarpal 3, including wrist.

Mandibular length (MNL).—Greatest length of mandible, from front of incisors to back of angular process.

Length of mandibular tooththrow (MNTL).—Alveolar length of mandibular tooththrow, from front of canine to back of M_3 .

Distance across maxillary tooththrows (MXD).—Greatest distance across upper molar rows, measured from labial sides of molars.

Length of maxillary tooththrow (MXTR).—Distance from anterior cingulum of canine to back of M^3 .

Length of phalanx 1 of digit 3 (P1D3).

Length of phalanx 2 of digit 3 (P2D3).

Length of tibia (TBL).

Length of tragus (TGL).—Length of tragus, from anterior basal point of origin to tip (measured on dry skins).

Length of tail (TL).

Zygomatic breadth (ZB).—Greatest distance across zygomatic arches.

Characters, other than standard external measurements and length of fur, were measured with dial calipers and rounded to the nearest 0.1 mm. Length of fur was taken with a millimeter rule, and values were rounded to the nearest millimeter. Measurements of the holotypes of *E. fidelis* and *E. argentinus* Thomas were made by Mr. J. E. Hill. Dr. G. Arbocco took measurements of the holotype of *E. dorianus*. Specimens examined are listed in the discussion section. All specimens are standard skins and skulls and are adult unless otherwise indicated. The acronyms designating the museums of deposition are defined by Choate and Genoways (1975), except for that of the British Museum of Natural History (BMNH).

Samples of males and females of *E. furinalis* from Brazil and from Paraguay were subjected to standard univariate analyses, employing *t*-tests (BMD13D, Dixon, 1976). The sexes of these and other samples of *E. furinalis* and *E. diminutus* were submitted as separate groups in a stepwise discriminant analysis (BMD07M, Dixon 1976). This multivariate analysis tested for sexual dimorphism within populations, and for differences within and between samples. Classification groups were from single localities, except for the Paraguayan samples of *E. furinalis* and for *E. d. diminutus*. The Paraguayan *E. furinalis* come from a relatively small and uniform geographic area (but were initially divided into two samples because of slight color differences). I pooled the two *E. d. diminutus* males to create a classification group for this taxon.

A second stepwise discriminant analysis included samples of *E. brasiliensis*, and additional samples of *E. diminutus* and *E. furinalis*, but utilized only 11 characters. This allowed the incorporation of some samples from Davis (1966) and of specimens with certain missing character values. I pooled the sexes in the samples in order to make all of the data comparable with those of Davis (1966). In this analysis, some obviously misclassified specimens, as determined in the first analysis, were submitted with their appropriate groups. In order to summarize the phenetic relationships among samples, individuals and sample means of short-haired *Eptesicus* from South America were subjected to a hierarchical cluster analysis (MINT), using average Euclidean distance as similarity coefficients. The phenogram was constructed using the unweighted pair-group method using arithmetic averages (UPGMA, Sneath and Sokal, 1973). The samples used in this analysis, their origin, and labels are as follows: 1.—*E. b. argentinus* females,

Table 1.—Morphometric traits of *Eptesicus*. Abbreviations are explained in the text.

Species	sex	N	TL	HBL	HF	EL	GSL	CB	ZB	MXTL	MXD
<i>E. brasiliensis</i>											
Catamarca, MSB 32725	♂	1	43	54	8.7	15.8	16.9	8.4	11.8	6.2	6.8
argentinus holotype	♀	1	—	—	—	—	17.3	8.2	12.3	6.3	7.6
melanopterus, CM	♀	1	35	58	8.0	13.0	17.2	8.9	10.5	6.1	7.6
<i>E. diminutus</i>											
fidelis holotype	♂	1	32	50	—	12.5	13.9	7.3	9.8	5.0	5.6
diminutus holotype	♂	1	37	51	10.0	—	14.3	6.6	9.4	5.1	5.8
Maranhão, FMNH 26452	♂	1	33	52	6.5	12.0	14.8	7.4	10.1	5.4	6.3
Minas Geraes, FMNH 20743	♀	1	42	45	7.5	13.2	15.0	7.5	9.6	5.4	6.1
Sao Paulo, MCZ 24821	♂	1	33	52	7.0	13.0	14.3	7.3	9.6	5.0	5.9
Tucumán, CM 42881*	♂	1	32	54	6.2	13.3	13.3	6.5	8.7	4.7	5.5
Tucumán, CM 42880	♀	1	35	54	6.8	13.5	13.8	6.7	9.1	5.0	5.7
Tucumán, CM 42882	♀	1	32	59	7.0	13.6	13.9	7.0	8.9	4.9	5.7
Uruguay, AMNH 205600	♂	1	32	56	6.0	11.0	13.5	6.9	9.0	5.0	6.0
Uruguay, AMNH & FMNH	♀	5	35	52	8.3	12.6	13.9	7.3	9.3	5.0	5.9
Range			33–37	51–53	7.8–9.0	12.0–13.0	13.3–14.7	7.0–7.5	9.1–9.7	4.9–5.1	5.8–6.0
<i>E. dorianus</i> holotype											
	♀	1	—	—	—	—	17.0	8.5	11.0	6.0	7.5
<i>E. furinalis</i>											
Brazil, CM	♂	5	39	57	6.6	13.2	16.1	7.9	10.7	5.7	6.6
Range			36–40	52–63	6.0–7.0	12.0–14.0	15.5–16.7	7.8–8.0	10.3–11.0	5.5–5.9	6.3–6.9
Brazil, CM	♀	7	38	59	6.6	14.1	16.1	7.9	10.8	5.8	6.6
Range			33–42	54–68	5.0–7.0	13.0–15.0	16.0–16.5	7.7–8.1	10.3–11.7	5.5–6.0	6.0–6.8
Bolivia, CM 2738	♂	1	40	55	8.0	12.0	15.4	7.4	9.8	5.5	6.2
Paraguay, BMNH 1.8.1.1	♂	1	36	54	—	—	15.2	7.0	9.8	5.3	6.1
Paraguay, UCOON 15649	♀	1	33	53	11.9	13.0	14.7	7.8	10.1	5.4	6.1
Paraguay, UMMZ	♂	7	39	54	9.3	14.6	15.5	7.7	10.4	5.6	6.4
Range			36–41	51–56	8.0–9.9	13.0–15.0	14.9–16.1	7.3–8.1	10.2–10.9	5.3–5.7	6.2–6.6
Paraguay, UCONN & UMMZ	♀	12	36	55	8.8	13.7	15.7	7.8	10.5	5.6	6.4
Range			35–40	52–63	8.0–9.9	12.0–15.0	15.0–16.8	7.4–8.3	9.9–11.7	5.4–6.0	6.2–6.6
Tucumán, CM 42883	♂	1	40	62	7.7	15.0	15.5	7.0	10.4	5.7	6.6
Tucumán, CM 42884	♀	1	41	70	8.9	15.2	16.9	7.7	11.3	6.0	6.8
Tucumán, CM 42885	♀	1	45	69	10.1	15.0	16.4	7.5	11.4	6.1	7.1
Tucumán, CM 42886*	♀	1	37	65	8.3	14.7	14.0	7.5	11.0	5.8	6.6

Table 1.—(Continued)

Species	sex	N	MNL	MNTL	FAL	M-III	P1D3	P2D3	FL	TBL	TGL
<i>E. brasiliensis</i>											
Catamarca, MSB 32725	♂	1	12.6	6.7	41.3	40.4	14.0	11.5	6	14.6	5.1
<i>argentinus</i> holotype	♀	1	12.9	7.2	45.5	42.0	15.0	12.0	—	—	—
<i>melanopterus</i> , CM	♀	1	12.7	6.4	39.3	36.5	12.9	11.8	5	—	4.7
<i>E. diminutus</i>											
<i>fidelis</i> holotype	♂	1	10.0	5.3	34.0	29.0	11.0	9.5	—	—	4.2
<i>diminutus</i> holotype	♂	1	10.0	5.6	35.7	33.0	12.6	9.8	—	14.3	4.5
Maranhão, FMNH 26452	♂	1	10.6	5.6	37.9	35.2	12.8	10.9	6	14.7	4.9
Minas Geraes, FMNH 20743	♀	1	—	5.8	36.0	33.5	13.1	10.6	5	14.2	5.0
Sao Paulo, MCZ 24821	♂	1	10.4	5.6	34.1	30.8	11.1	9.6	5	12.9	4.5
Tucumán, CM 42881*	♂	1	9.5	5.0	32.1	30.1	10.3	9.0	5	11.8	4.0
Tucumán, CM 42880	♀	1	10.0	5.2	32.6	31.5	10.4	9.4	5	12.5	4.5
Tucumán, CM 42882	♀	1	10.2	5.2	33.6	31.3	11.2	9.3	5	12.7	4.2
Uruguay, AMNH 205600	♂	1	10.2	5.2	31.5	30.5	10.7	9.1	5	—	—
Uruguay, AMNH & FMNH	♀	5	10.3	5.3	32.4	30.2	10.8	8.9	6	11.7	4.2
Range			10.2–10.5	5.2–5.5	31.5–32.4	28.5–30.8	10.4–11.5	8.6–9.6	5–6	11.5–11.8	4.0–4.5
<i>E. dorianus</i> holotype	♀	1	12.6	6.8	41.0	38.5	14.5	13.0	—	—	—
<i>E. furinalis</i>											
Brazil, CM	♂	5	12.0	5.9	39.0	37.8	13.8	11.4	6	14.2	4.7
Range			11.6–12.3	5.7–6.2	37.5–41.1	35.9–39.5	13.4–14.6	10.6–12.3	5–6	13.1–15.0	4.8–5.1
Brazil, CM	♀	7	12.4	6.0	40.0	38.2	14.7	11.9	6	15.0	4.9
Range			12.0–12.7	5.8–6.1	38.9–41.9	37.3–39.3	14.4–15.5	11.0–12.9	4–6	14.4–15.9	4.7–5.2
Bolivia, CM 2738	♂	1	11.8	5.7	38.2	35.6	13.8	11.8	6	14.3	4.0
Paraguay, BMNH 1.8.1.1	♂	1	11.3	5.8	36.3	34.5	12.0	9.5	—	—	—
Paraguay, UCONN 15649	♀	1	11.3	5.7	34.8	34.2	12.1	9.9	7	—	4.4
Paraguay, UMMZ	♂	7	11.5	5.9	37.4	35.7	13.1	10.9	6	14.9	4.9
Range			10.9–11.8	5.5–6.7	35.8–39.3	34.4–36.9	11.9–14.2	10.0–11.9	5–7	14.1–16.1	4.5–5.1
Paraguay, UCONN & UMMZ	♀	12	11.7	6.0	37.4	36.2	13.3	11.0	6	14.0	4.6
Range			11.0–12.4	5.7–6.4	34.3–39.8	32.9–38.9	12.1–15.1	10.3–12.3	5–7	12.1–15.1	4.3–5.2
Tucumán, CM 42883	♂	1	11.9	6.2	39.3	38.1	14.0	12.5	6	14.9	5.0
Tucumán, CM 42884	♀	1	12.6	6.5	41.1	39.5	15.1	12.9	7	15.8	5.3
Tucumán, CM 42885	♀	1	12.8	6.7	39.8	38.1	15.4	12.3	7	16.0	5.2
Tucumán, CM 42886*	♀	1	11.9	6.4	39.7	33.6	13.0	10.3	7	14.5	4.5

* Juvenile.

mean values of three specimens from Davis (1966); 2.—*E. b. argentinus* male from Catamarca, MSB 32725; 3.—*E. b. brasiliensis* males, mean values of two specimens from Davis (1966); 4.—*E. b. melanopterus*, mean values of 20 specimens from Davis (1966); 5.—*E. b. melanopterus* male from Surinam, CM (uncatalogued); 6.—*E. b. thomasi*, mean values of 20 specimens from Davis (1966); 7.—*E. b. thomasi* holotype; 8.—*E. b. argentinus* holotype; 9.—*E. dorianus* holotype; 10.—*E. innoxius* males, mean values of four specimens from Davis (1966); 11.—*E. innoxius* females, mean values of 13 specimens from Davis (1966); 12.—*E. diminutus* holotype; 13.—*E. diminutus* male from Maranhão, FMNH 26492; 14.—*E. diminutus* female from Minas Geraes, FMNH 20743; 15.—*E. diminutus* male from São Paulo, MCZ 24821; 16.—*E. d. fidelis* holotype; 17.—*E. d. fidelis* male from Uruguay, AMNH 20960; 18.—*E. d. fidelis* females from Uruguay, mean values of five specimens, AMNH and FMNH; 19.—*E. d. fidelis* females from Tucumán, mean values of two specimens, CM; 20.—*E. f. furinalis* male from Paraguay, BMNH 1.8.1.1; 21.—*E. f. gaumeri* holotype; 22.—*E. f. gaumeri*, mean values of nine specimens from Davis (1966); 23.—*E. f. chapmani* holotype; 24.—*E. f. chapmani*, mean values of 21 specimens from Davis (1966); 25.—*E. f. furinalis* female from Jujuy, AMNH 180305; 26.—*E. f. furinalis*, mean values of 33 specimens from Davis (1966); 27.—*E. furinalis* male from Tucumán, CM 42883; 28.—*E. furinalis* females from Tucumán, mean values of two, CM; 29.—*E. f. chapmani* male from Bolivia, CM 2738; 30.—*E. f. chapmani* males from Brazil, mean values of five, CM; 31.—*E. f. chapmani* females from Brazil, mean values of seven, CM; 32.—*E. f. furinalis* males from Paraguay, mean values of five, UMMZ; 33.—*E. f. furinalis* females from Paraguay, mean values of 12, UCONN and UMMZ.

Chromosome preparations of humeral marrow cells were made using the *in vivo* colchicine, hypotonic sodium-citrate technique. Procedures and nomenclature follow Patton (1967).

RESULTS

Females averaged larger than males in most characters (Table 1), although few of the differences were significant. Females of *E. furinalis* from Crato, Ceara, Brazil, were significantly larger than males in mandibular length ($P = 0.03$) and length of phalanx 1 of digit 3 ($P = 0.03$). There were no significant differences between the Paraguayan samples of *E. furinalis*. Females and males were readily distinguishable by the discriminant function analysis, and there was no misclassification of the sexes in the samples of *E. furinalis*. Table 2 presents the results of discriminant analysis I, based upon 16 morphometric traits. Note that males and females of the Brazilian and Paraguayan populations are most similar to each other. Thus, although the sexes are distinctive, the populations form discreet morphological units. Table 3 lists the characters used in this analysis and orders them from the most to the least useful for distinguishing groups.

Canonical analysis provides a mechanism of graphically portraying the phenetic relationships among these samples (Fig. 1). The first two canonical variates account for 71.2% of the total dispersion (Variate I = 44.9%). Note in Fig. 1 that the sexes are readily separable except for one female of *E. furinalis*, which is plotted among the males. This specimen is, however, closest to the other females. The Brazilian samples of *E. furinalis* are distinct from those from Paraguay, and the

Table 2.—Mean squared Mahalanobius distance values (D^2) of *Eptesicus* samples, based upon the linear discriminant function of Analysis I.

	Samples	Samples										
		2	5	7	8	9	10	11	13			
<i>diminutus</i>												
1.	<i>fidelis</i> holotype	56.0	103.7	167.1	205.7	112.7	146.7	135.5	266.8			
2.	<i>diminutus</i> males	9.7	97.0	114.5	135.9	60.8	86.3	80.8	177.2			
3.	<i>diminutus</i> female	154.4	190.3	153.0	163.4	142.7	214.8	186.5	212.0			
4.	São Paulo male	50.5	46.7	78.8	112.7	61.6	90.8	83.8	153.1			
5.	Tucumán females	91.9	4.1	99.4	135.9	116.5	126.9	161.4	176.2			
<i>furinalis</i>												
6.	UCONN 15649, female	101.1	111.5	71.9	104.2	40.0	30.7	46.4	192.8			
7.	Brazil males	118.0	108.8	13.5	26.0	55.0	48.5	69.8	76.4			
8.	Brazil females	140.4	145.5	26.5	13.7	68.6	69.7	96.1	58.4			
9.	Paraguay, UMMZ males	64.1	125.5	54.4	67.7	13.0	28.7	44.1	109.3			
10.	Paraguay, UMMZ females	89.7	133.8	48.1	69.1	28.8	13.1	38.0	118.6			
11.	Paraguay, UCONN females	86.6	172.8	71.8	97.9	46.6	41.4	15.5	162.6			
12.	Tucumán male	153.5	137.8	71.5	60.1	24.7	130.9	156.1	36.2			
13.	Tucumán females	173.8	178.3	69.1	58.9	102.5	111.7	153.2	6.2			

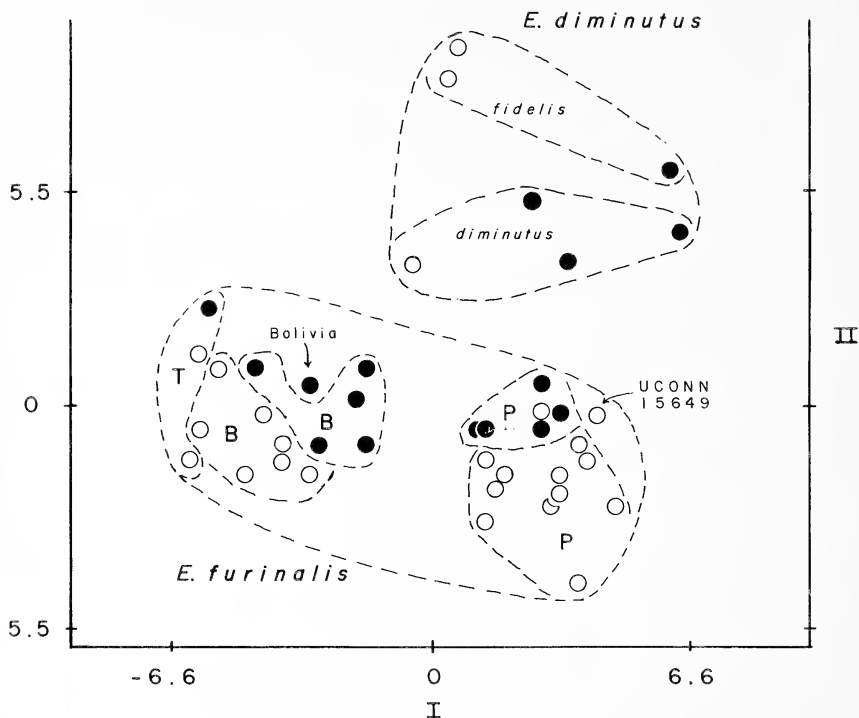


Fig. 1.—Bivariate plot of canonical variates I and II for samples of *E. diminutus* and *E. furinalis*. Open circles = females; closed circles = males; B = Brazil; P = Paraguay; T = Tucumán.

specimens of *E. furinalis* from Tucumán Province, Argentina, and from Bolivia are phenetically most similar to the Brazilian samples (Fig. 1 and Table 2). The Paraguayan specimen of *E. cf. fidelis* (UCONN 15649) of Wetzel and Lovett (1974), is assigned to *E. furinalis* (Table 2 and Fig. 1).

The variables with the highest positive canonical coefficients for Variate I (arbitrarily, those with values greater than 1.0), include, in order of decreasing values, cranial breadth, length of maxillary tooth-row, zygomatic breadth, and length of hind foot. The larger negative coefficients, in descending order, are mandibular length, distance across the molar rows, and greatest length of skull. Size has relatively little influence on Variate I. The only character with a positive coefficient for Variate II, greater than 1.0, was length of maxillary tooth-row. Negative coefficients with values less than -1.0 are distance across the molar rows, mandibular length, zygomatic breadth, length of phalanx 1 of digit 3, and length of hind foot. The smallest bats were

Table 3.—Variables used in the discriminant function analyses, listed in order of their usefulness in distinguishing groups. The character with the greatest between groups variance and the least within groups variance is selected first. Other traits are ranked using the same criteria. The statistics are recalculated at each step.

Step	Discriminant Analysis I			Discriminant Analysis II		
	Trait	F-value	U-statistic	Trait	F-value	U-statistic
1.	MNL	25.14	0.1373	MXTL	38.85	0.1207
2.	HFL	11.91	0.0336	MNL	7.99	0.0477
3.	CB	4.16	0.0158	MNTR	4.62	0.0251
4.	HBL	4.21	0.0073	P1D3	3.61	0.0146
5.	MNTL	2.39	0.0043	CB	2.77	0.0093
6.	TBL	2.38	0.0025	MXD	2.82	0.0058
7.	P1D3	1.86	0.0016	FAL	2.59	0.0038
8.	TL	2.26	0.0009	P2D3	2.06	0.0026
9.	ZB	3.07	0.0004	M-III	1.68	0.0019
10.	FAL	1.25	0.0003	ZB	1.47	0.0014
11.	MXTL	0.87	0.0002	GSL	0.45	0.0013
12.	MXD	0.78	0.0002			
13.	TGL	0.74	0.0001			
14.	M-III	0.78	0.0001			
15.	P2D3	0.69	0.0000			
16.	GSL	0.79	0.0000			

positioned at the positive end, and larger animals at the negative end of Variate II.

The results of the second discriminant function/canonical analysis are presented in Table 4 and Fig. 2. In this analysis the sexes were pooled, the character suite was reduced to 11, and additional samples, including *E. brasiliensis*, were added. The sexes are generally identifiable within samples, and overlap between taxa typically involves males of the larger OTU and females of the smaller OTU (Fig. 2). The variables utilized in this analysis are presented in Table 3. Variables with the highest positive coefficients for Variate I (those with values greater than 1.0) are distance across the molar rows and length of mandibular tooththrow. High negative coefficients were not scored for Variate I. For Variate II, length of mandibular tooththrow and length of maxillary tooththrow had high positive coefficients, and mandibular length had a high negative coefficient. Canonical Variate I appears to be strongly influenced by size, with small bats positioned on the negative pole and large bats on the positive pole.

The holotype of *E. dorianus* falls within the distribution of *E. brasiliensis argentinus* for Canonical Variates I and II (Fig. 2), and is closest, overall, to *E. brasiliensis melanopterus* (Jentink) in terms of its position on the linear discriminant functions (Table 4). The specimen from Villa Rica, Depto. Villarrica, Paraguay (BMNH No. 1.8.1.1, *E.*

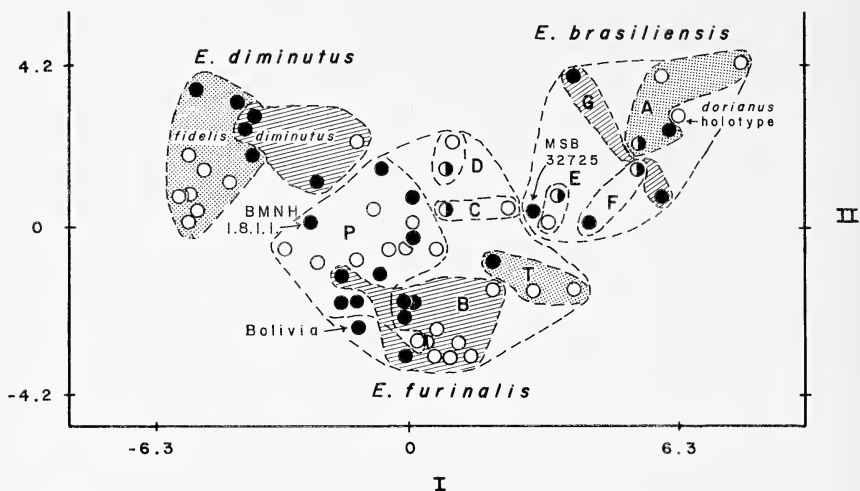


Fig. 2.—Bivariate plot of canonical variates I and II for samples of *E. brasiliensis*, *E. diminutus*, and *E. furinalis*. Open circles = females; closed circles = males; half open circles = sex unknown or samples of mixed sexes; A = *E. b. argentinus*; B = *E. f. chapmani* from Brazil; C = *E. f. chapmani* from Davis (1966); D = *E. f. furinalis* from Davis (1966); E = *E. b. melanopterus*; F = *E. b. thomasi* from Davis (1966); G = *E. b. brasiliensis* from Davis (1966); P = *E. f. furinalis* from Paraguay; T = *E. furinalis* from Tucumán. See text for further explanation.

dorianus of Davis, 1966), is placed within the sample of Paraguayan *E. furinalis* (Table 4 and Fig. 2). Measurements from Davis (1966) of *E. f. furinalis* are somewhat intermediate to the samples of *E. furinalis chapmani* Allen and to samples of *E. furinalis* from Paraguay and from Tucumán, Argentina. This is not surprising, as the one specimen (AMNH 180305) is from northwestern Argentina (Jujuy Province), near the range of *E. f. chapmani*, and the sample means included specimens from northwestern Argentina and from several localities in Paraguay (Davis, 1966). There is a near continuum of variation in these samples (Fig. 2). If, however, one looks at potentially sympatric populations, there is a clearer separation of taxa. In Fig. 2, the stippled areas indicate the positions of three sympatric populations in northwestern Argentina, and the lined areas signify the three potentially sympatric populations in Brazil. The separation of *E. f. chapmani* and

Fig. 3.—Phenogram of South American short-haired *Eptesicus* species, computed from average Euclidean distance values and clustered by the unweighted pair-group method using arithmetic averages (UPGMA). The numbers designating taxa and localities are defined in the text. The cophenetic correlation coefficient for the phenogram is 0.737.

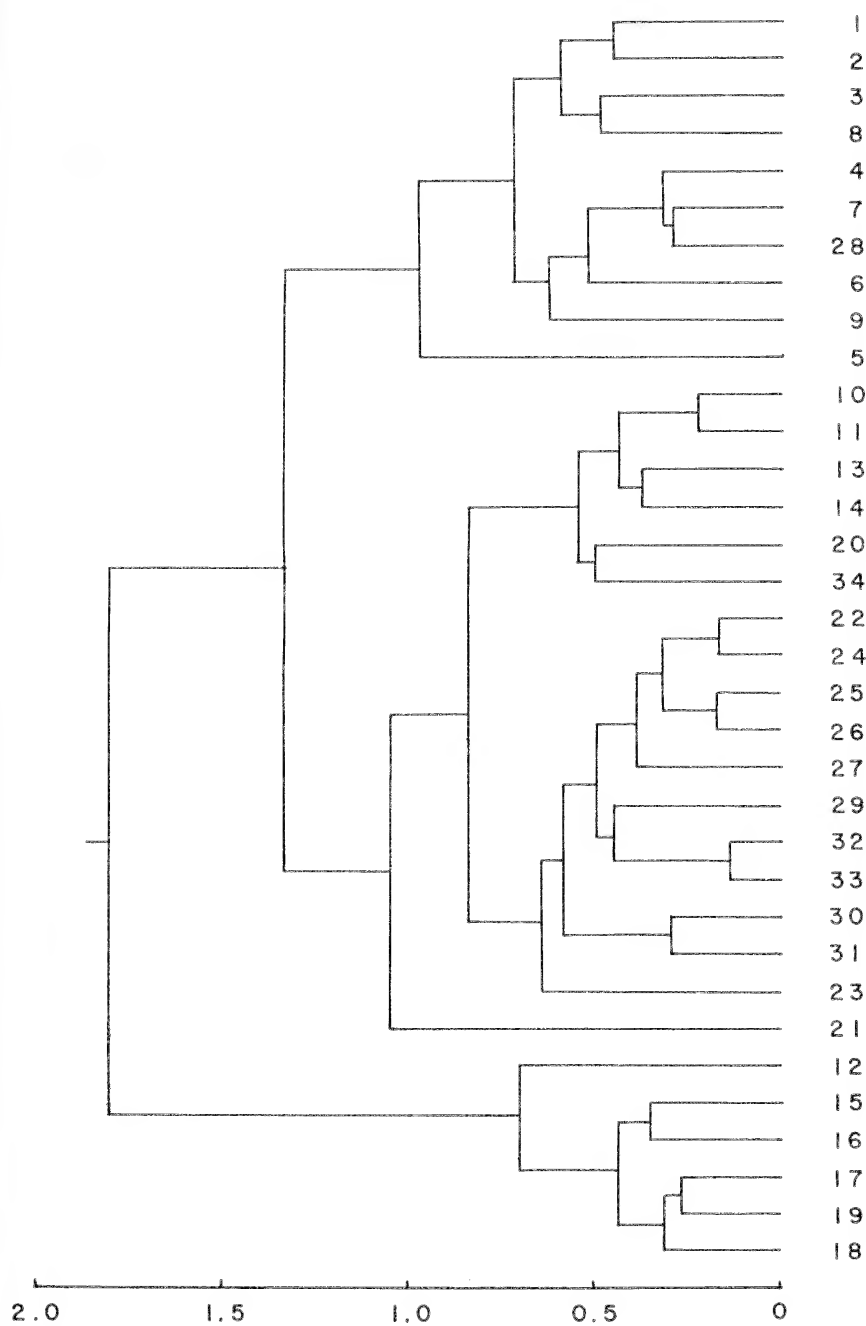


Table 4.—Mean squared Mahalanobis distance values (D^2) of *Eptesicus* samples, based upon the linear discriminant function of Analysis II.

Samples	Samples													
	1	2	3	4	7	8	9	11	13	14				
<i>brasiliensis</i>														
1. <i>argentinus</i>	8.9	26.9	42.7	39.0	151.9	171.6	106.9	83.4	81.3	56.7				
2. <i>brasiliensis</i>	23.6	5.6	37.8	35.2	123.3	135.7	74.2	59.5	58.7	47.9				
3. <i>melanopterus</i>	45.6	43.9	11.7	26.2	94.6	112.3	75.0	41.8	44.3	35.2				
4. <i>thomasi</i>	36.4	35.9	20.7	6.3	119.9	129.6	89.6	53.0	60.7	28.6				
5. Catamarca, MSB 32725	32.2	24.3	40.1	53.1	87.0	98.4	56.6	33.7	27.1	41.8				
<i>dorionus</i>														
6. holotype	124.8	147.9	118.5	143.7	252.3	298.5	232.0	200.0	185.3	129.7				
<i>diminutus</i>														
7. <i>fidelis</i> , Uruguay*	152.3	127.1	92.2	122.9	9.3	16.8	24.8	58.0	34.3	91.5				
8. <i>fidelis</i> , Tucumán	165.3	132.6	103.1	125.8	10.1	2.6	20.0	55.6	34.6	94.0				
9. <i>diminutus</i>	105.4	76.0	70.6	90.7	22.8	24.8	7.3	41.8	23.3	65.3				
<i>furinalis</i>														
10. BMNH 1.8.1.1	109.8	92.6	65.9	84.1	20.6	23.1	27.6	29.3	18.3	46.9				
11. Brazil	84.2	63.6	39.8	56.5	58.4	62.8	44.2	9.5	16.8	30.0				
12. Bolivia	119.1	84.6	50.0	61.8	39.2	38.6	36.7	14.2	20.3	34.6				
13. Paraguay	82.7	63.3	42.8	64.6	35.2	42.3	26.2	9.5	37.4	35.2				
14. Tucumán	54.2	48.6	29.9	28.7	88.5	97.8	64.3	26.7	33.6	64.0				
15. Yuto, Jujuy	47.3	32.6	29.7	30.1	43.5	49.6	22.5	32.1	21.3	20.5				
16. <i>furinalis</i> , mean	51.5	32.4	28.8	31.9	42.6	45.0	17.8	22.8	15.4	17.5				
17. <i>chapmani</i> , holotype	58.1	43.1	26.6	24.1	79.4	80.7	47.9	37.1	35.3	20.6				
18. <i>chapmani</i> , mean	56.3	36.6	21.2	28.0	44.7	50.4	22.6	18.0	13.8	12.7				

* Includes the holotype of *fidelis*.

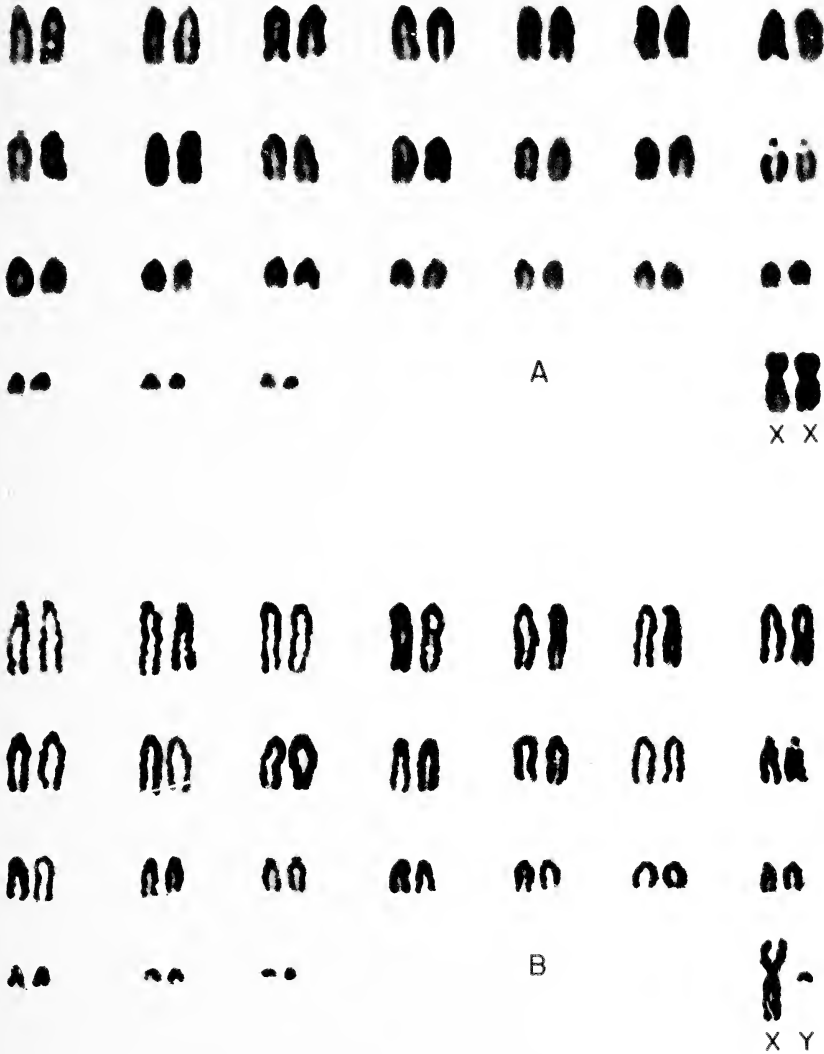


Fig. 4.—Karyotypes of *Eptesicus*. A, *E. furinalis* female from Aguas Chiquitas, about 800 m, Sierra de Medina, Provincia Tucumán, Argentina, CM 42886; B, *E. diminutus* male from Aguas Chiquitas, about 800 m, Sierra de Medina, Provincia Tucumán, Argentina, CM 42881.

E. b. melanopterus from Amazonia is less satisfactory (Fig. 2 and Table 4), and the relationships of these taxa to those of other populations of *E. brasiliensis* and *E. furinalis* are poorly resolved by this analysis.

The results of the hierarchical cluster analysis (UPGMA) are presented in Fig. 3. Note in the phenogram that there are three main clusters, representing, from top to bottom, big bats (primarily *E. brasiliensis*), intermediate-sized bats (*E. innoxius*, *E. furinalis*, and two *E. diminutus*), and small bats (*E. diminutus*). The intermediate-sized bat cluster is divisible into two distinct units—an *E. furinalis* cluster and a cluster of relatively small bats, including *E. innoxius*, two small *E. furinalis*, and two large *E. diminutus* specimens. These two *E. furinalis* specimens are the two to the far left in the *E. furinalis* cluster of Fig. 2. The two *E. diminutus* specimens are the two on the extreme right in the *E. d. diminutus* cluster of Fig. 2. The male of *E. furinalis* from Tucumán is closely linked with *E. furinalis* specimens from north-western Argentina in this UPGMA analysis (Fig. 3), but the females are linked with *E. b. thomasi* and *E. b. melanopterus*. This reflects the relatively large size of this sample of *E. furinalis* females.

The 50 chromosomes of *E. furinalis* and *E. diminutus* are identical in gross morphology, and consist of 48 acrocentric autosomes ($2N = 50$, $FN = 48$), with a large submetacentric X and a small acrocentric Y. One pair of intermediate-sized autosomes has a subcentromeric secondary construction (Fig. 4).

DISCUSSION

The karyotypes of *E. furinalis* and *E. diminutus* appear identical in gross morphology to the North American forms, *E. furinalis gaumeri* J. A. Allen, *E. andinus*, and *E. fuscus* (Baker and Patton, 1967), to the Caribbean species, *E. guadeloupensis* Genoways and Baker (1975), and to the Old World species, *E. serotinus* (Schreber) (Baker et al., 1974; Fedyk and Fedyk, 1970) and *E. hottentotus* (A. Smith) (Peterson and Nagorsen, 1975). This eptesicoid karyotype is also identical in appearance to that of the South American big-eared bat, *Histiotus montanus* (Philippi and Landbeck) (Williams and Mares, 1978). The only variation in this eptesicoid karyotype noted to date is in the morphology of the Y chromosome of *E. serotinus* from Poland, which have a submetacentric Y rather than the typical acrocentric Y (Fedyk and Fedyk, 1970). It is of particular note that the small South American species, *E. furinalis* and *E. diminutus*, exhibit the eptesicoid karyotype, whereas the small African species, *E. capensis* (A. Smith), has a karyotype consisting of a $2N$ of 32 and an FN of 50 (Peterson and Nagorsen, 1975). This latter karyotype appears most similar to those of several species of *Pipistrellus* (Capanna and Civitelli, 1970).

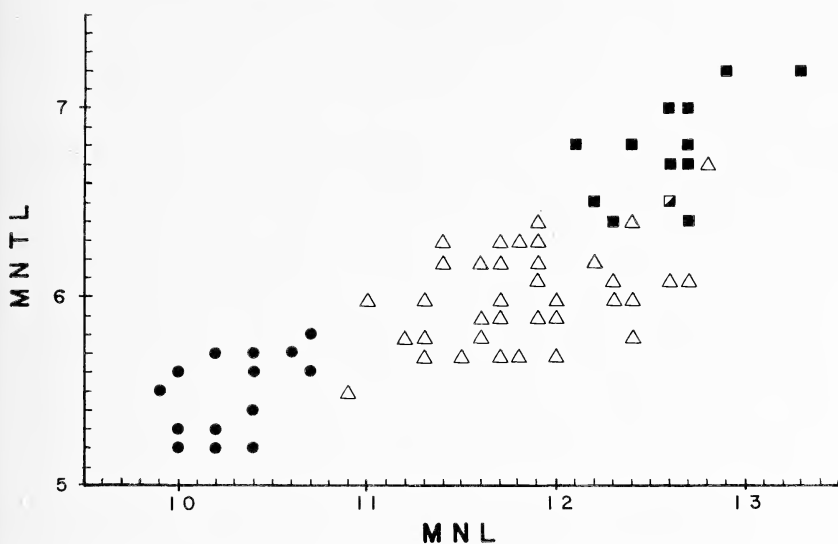


Fig. 5.—Bivariate plot of mandible length (MNL) and mandibular tooththrow length (MNTL) for individuals of *Eptesicus*. Circles = *E. diminutus*; triangles = *E. furinalis*; squares = *E. brasiliensis*.

Sexual size dimorphism in *E. furinalis* and *E. diminutus* is apparent. As is the typical pattern in vespertilionid bats (Williams and Findley, 1979), females average larger than males. These size differences have apparently been a major reason for species misidentification. Small males of *E. furinalis* can be confused with the larger females of *E. diminutus*. *E. brasiliensis* is probably also size dimorphic, although the samples utilized in this study were not all identifiable by sex. Misidentification between *E. furinalis* and *E. brasiliensis* would most likely involve large *E. furinalis* females and small *E. brasiliensis* males.

The overlap in size in these three species makes it difficult to characterize the species. This size continuum is well illustrated by plotting mandibular length against length of mandibular tooththrow (Fig. 5). These are two of the best characters for distinguishing species (see Table 3), but they cannot distinguish all specimens. Other than a complex linear discriminant function (which separates most populations of these species), there is no single characteristic, among the ones studied, that will distinguish all *E. diminutus*, *E. furinalis*, and *E. brasiliensis*. There should be relatively good size differences, however, between these short-haired species in any single area. In identifying specimens, it is essential that they are properly sexed. When measuring mandibular length, one must be certain that the angular process of the mandible is intact. Length of forearm of adult specimens should

prove sufficiently reliable to identify most specimens in the field (see Table 1 and Davis, 1966).

Eptesicus brasiliensis

There may be some question as to the identity of the specimen from Potrero Dike, El Potrero, Catamarca Province, Argentina (MSB 32725), designated as *E. brasiliensis* (see Tables 1 and 4, and Fig. 3). It is structurally most similar to the *brasiliensis* complex, but is somewhat smaller than other *E. brasiliensis*. As the other included individuals of *E. b. argentinus* are females or of unknown sex, its smaller size may simply reflect one extreme of normal variation. It does appear to be quite similar in dimensions to a specimen from nearby Mendoza (Massoia, 1976), which I consider to be *E. brasiliensis*. The long, subacute tragus of MSB 32725 is unlike any *Eptesicus* I have seen, but I do not know if this tragus shape is characteristic for some populations of *E. brasiliensis*.

The samples of *E. brasiliensis melanopterus* consist of a male from Keizerstraat, Paramaribo, Surinam (CM), the type locality for *E. melanopterus* (Jentink), and the means of a sample reported by Davis (1966). This latter sample was identified as *E. furinalis* by the discriminant function analysis, and was linked with a cluster consisting of the *E. b. thomasi* Davis holotype and the females of the Tucumán sample of *E. furinalis* in the UPGMA analysis (Fig. 3). It is possible that this sample contains individuals of both *E. furinalis* and *E. b. melanopterus*. The topotype of *E. b. melanopterus* is the most distinctive of the *E. brasiliensis* cluster in the UPGMA analysis. It has a greatly inflated braincase and a large sagittal crest. The crest is unusual for a bat the size of *E. b. melanopterus* (which is similar in size to *E. furinalis*). The specific status of *E. b. melanopterus* and the systematic relationships of *Eptesicus* populations from Amazonia and the northern South American lowlands are, in my opinion, still unresolved.

Eptesicus furinalis

The outlines of the phenetic relationships of the South American populations of *E. furinalis* (*E. f. gaumeri* excluded) are clear, although many details must still be worked out as adequate material becomes available. Individuals from the Rio Paraná/Rio Uruguay and Chaco Boreal lowlands are small for *E. furinalis* (Table 1) and are nearly black in color (in fresh pelage), although in the western Chaco of Paraguay they are browner. The name *E. f. furinalis* (D'Orbigny) applies to this population. Intermediate-sized bats from Amazonia, and from the lower Andean slopes in Bolivia form a second morphologic unit, *E. f. chapmani*. Specimens from the Caatinga region of Brazil seem most closely related to *E. f. chapmani* (Figs. 2 and 3). Bats from the

higher, mixed mesic Chaco region of Tucumán, Salta, and Jujuy provinces, Argentina, are large, and are brownish chestnut or auburn in color. They are more similar to *E. f. chapmani* than to the geographically adjacent *E. f. furinalis* (Tables 1, 2, and 4; Figs. 1–3). This population is distinctive, and is hereby named.

***Eptesicus furinalis findleyi*, new subspecies**

Holotype.—Adult female; skin, skull, and chromosomes, CM 42884; from Aguas Chiquitas, about 800 m, Sierra de Medina, Provincia Tucumán, Argentina; obtained 29 December 1975 by D. F. Williams, original no. 2044.

Distribution.—Known from along the eastern Andean foothills, from Tucumán, northward in Jujuy and Salta provinces, Argentina.

Diagnosis.—A large, chestnut or auburn brown member of the *E. furinalis* complex. Hairs on underparts light buffy-tipped. Membranes, ears, and lips dark brownish-black. Fur intermediate in length.

Etymology.—This population is respectfully named for James S. Findley, in honor of his many contributions to chiropteran biology.

Description.—Size intermediate for *Eptesicus* and large for *E. furinalis* (see Table 1). Color above between Chestnut and Auburn (Ridgway, 1912), with a glossy sheen; hairs blackish basally. Underparts with light buffy-tipped hairs (closest to Warm Buff, Ridgway, 1912); hairs blackish basally except for the posterior pelvic region, where they are buffy throughout their length. Dorsal pelage of intermediate length, averaging about 7 mm. Membranes, lips, and ears dark brownish-black; membranes naked. Tragus relatively long, with a rounded and anteriorly inflected tip. Skull with weakly developed sagittal crest (Fig. 6). Karyotype of typical eptesicoid pattern, with a 2N of 50, and 48 autosomal arms; autosomes all acrocentric; one pair of intermediate-sized autosomes with a subcentromeric heterochromatic band; X chromosome large and submetacentric; Y chromosome small and acrocentric (Fig. 4).

Comparisons.—*Eptesicus furinalis findleyi* is larger than *E. f. furinalis* (see Table 1), is brownish-chestnut or auburn rather than brownish-black, has a glossy sheen to the fur, and has a relatively longer tragus and smaller hind foot. From *E. f. chapmani*, *E. f. findleyi* can be distinguished by its richer chestnut or auburn brown color with a glossier sheen, its buffy rather than grayish underparts, and by its larger size (Table 1).

Remarks.—Specimens from Jujuy and Salta provinces are somewhat intermediate (that is, they are smaller and darker than *E. f. findleyi* from Tucumán) to both *E. f. chapmani* and *E. f. furinalis*. This is especially true of specimens from Yuto, Jujuy.

Specimens examined.—ARGENTINA. *Jujuy*: Ledesma, 1♂ (AMNH); Santa Barbara, 1♂, 1♀ (AMNH); Yuto, 11♂, 8♀ (AMNH). *Salta*: 24 km NW Agua Blanca, Departamento Orán, 1♂ (MSB). *Tucumán*: Aguas Chiquitas, about 800 m, Sierra de Medina, 1♂, 3♀ (1 juvenile) + chromosomes (CM).

Referred material.—ARGENTINA. *Jujuy*: Palma Sola, 550 m (Villa-R. and Cornejo,

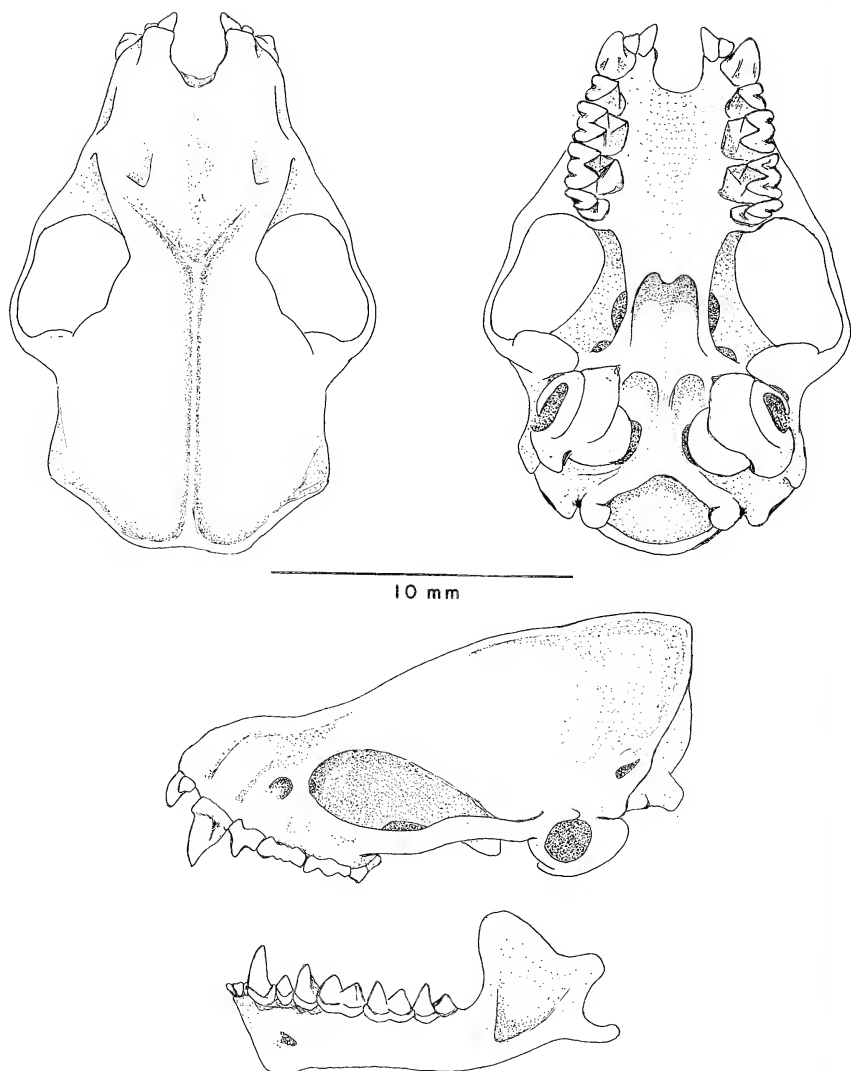


Fig. 6.—Skull of *Eptesicus furinalis findleyi*. A camera lucida drawing, based upon the holotype (CM 42884).

1969). Tucumán: Concepcion, 1 ♀ (BMNH); Tucumán, 450 m, 1 ♂ (BMNH) (Davis, 1966).

Comparative material of *E. furinalis*, examined and referable to other subspecies are listed below:

E. furinalis furinalis.—PARAGUAY. Boquerón: line camp, Juan de Zalazar, 1 ♀ (UConn); 0.75 km N line camp, Juan de Zalazar, 1 ♀ (UConn); 3 km SE line camp,



Fig. 7.—Distribution of *Eptesicus diminutus*. Type localities are designated by two concentric circles. Open circles = *E. d. diminutus*; solid circles = *E. d. fidelis*.

Rio Verde, Juan de Zalazar, 1♀ (alc.) (UCONN); 4 km N Rio Verde, Juan de Zalazar, 1♀ (UCONN). *Caaguazú*: Sapucay, 4♂, 7♀ (AMNH). *Central*: Asunción, 1♀ (UMMZ); Asunción, Recoleta, 5♂, 4♀ (1 skull only) (UMMZ); San Lorenzo, 1♀ (UCONN). *Cordillera*: Tobati, 1♂ (UCONN). *Cznendeyó*: 6.3 km NE Curuzuabá, 1♂ (UMMZ). *Guaira*: Itapé, 2♂ (AMNH). *Itapúa*: 1 km N Rio Paraná, left bank Rio Pirapó, 2♂ (alc.) (UCONN). *Neuva Asunción*: 49.6 km N (by Rd.) Filadelfia, 1♂ (UMMZ).

E. furinalis chapmani.—BRAZIL. *Amazonas*: Rio Negro, Igarapé Cação Pereira, near Manaus, 3♂, 1♀ (AMNH); Rio Madeira, Rasarinho, Lago Miguel, 1♂ (AMNH). *Ceara*: Foresta Nacional de Araripe, Crato, 6♂ (1 juvenile), 8♀ (1 juvenile) (CM—uncataloged). BOLIVIA. *Santa Cruz*: Provincia del Sara, 1♂ (CM).

Eptesicus diminutus

The smallest South American *Eptesicus*, *E. diminutus*, is found in the Rio Paraná/Rio Uruguay lowlands, in the mixed mesic Chaco region of Tucumán, Argentina, and the eastern Brazilian highlands from Maranhão to São Paulo (Fig. 7). The lowland population was named *E. fidelis* by Thomas (1920), who considered *E. dorianus* to be a synonym of *E. furinalis* on the basis of Dobson's (1885) measurements. Subsequently, *E. fidelis* was synonymized with *E. dorianus* by Davis (1966), who concluded that those measurements placed *E. dorianus* within the size range of the smallest *Eptesicus*. Davis' (1966) characterization of this species was based upon a series of specimens that included a male *E. furinalis* (BMNH 1.8.1.1) as well as upon Dobson's (1885) measurements of the holotype of *E. dorianus*. Measurements of the holotype of *E. dorianus* (Table 1), provided by Dr. Arbocco, show this specimen to be too large to be either *E. diminutus* or *E. furinalis*. The multivariate analyses (Table 4 and Figs. 2 and 3) place this specimen with *E. brasiliensis*, but it is not an especially close association. As the measurements of the holotype do not correspond to those of Dobson (1885), a mixup is evident. Measurements of the holotype, followed by Dobson's (1885) measurements of the same specimen (converted from inches and tenths to millimeters) are as follows: length of forearm, 41 (36.8); length of metacarpal 3, 38.5 (33.0); length of phalanx 1 of digit 3, 14.5 (11.4). Obviously, the specimen now designated as the holotype may not be the one upon which Dobson based his description of *E. dorianus*. An alternate explanation, however, is that Dobson somehow erred in recording or transcribing the measurements. That this is a possibility is suggested by the fact that he explicitly compares *E. dorianus* with *E. hilarii* (Geoffroy), stating "about the size of *V. hilarii* which it closely resembles in the form of the ears and teeth but differs from in its shorter tail and ears (the forearm being the same length in both species)" (Dobson, 1885). The name *E. hilarii* was generally applied to populations of *E. brasiliensis* at the time Dobson described *E. dorianus*.

I believe that, on the basis of Dobson's measurements, *E. dorianus* (Dobson, 1885) is a junior synonym of *E. furinalis* (D'Orbigny, 1847).

However, if the specimen presently designated as the holotype can be shown to be the one that Dobson described, then the name *E. dorianus* may apply to the population now known as *E. brasiliensis argentinus* Thomas, 1920. Alternately, the holotype may be an Old World *Eptesicus*, a mixup in specimens occurring either prior to, or after Dobson described *E. dorianus*. Perhaps the best way to treat the name *E. dorianus* (Dobson), and the one I prefer, is to designate it as a *nomen dubium*, as it cannot be applied with certainty to any known taxon.

E. diminutus fidelis from the lowlands of the Rio Paraná and Rio Uruguay are slightly larger and are a more Buffy-Brown (Ridgway, 1912) than specimens from Tucumán. The tips of the hairs are particularly light buffy, creating a slightly frosted appearance dorsally. Ventrally, the hairs are very light grayish-tipped, giving a whitish cast to the underparts. The membranes are dark grayish or blackish. Specimens from Tucumán are truly diminutive (Table 1) and are uniquely colored, being bright, glossy brown above, between Auburn and Chestnut of Ridgway (1912). The coloration below is buffy, and the membranes are brownish-black. This population appears to be distinctive, but an adequate assessment of individual and geographic variation cannot yet be made.

In Brazil is a third population, *E. d. diminutus*. These bats are larger than *E. d. fidelis* (Table 1) and are more brownish in color. The only known female of this race approaches the smaller males of *E. f. furinialis* in size (Table 1 and Figs. 1 and 3). The holotype (from São Marcello, Rio Preto, Bahia, Brazil, Osgood, 1920) is similar to the specimens of *E. diminutus fidelis* (Figs. 2 and 3). The specimen from São Paulo is the darkest of this species I have seen, appearing slightly darker and with a more reddish tone than the color Warm Sepia of Ridgway (1912). Its underparts are several shades lighter (with buffy tips to the hairs), and the membranes are blackish. Conversely, the specimen from Maranhão is the lightest brown of the species, between Sanford's Brown and Auburn. The UPGMA analysis places the São Paulo specimen (MCZ 24821) closest to the holotype of *E. d. fidelis* (Fig. 3). In contrast, discriminant function/canonical analysis II places that specimen closest to the *E. diminutus* holotype (Fig. 2, Table 4). In the first discriminant function analysis, this specimen was positioned intermediate to the holotypes of *E. d. diminutus* and *E. d. fidelis* (MCZ 24821 is the uppermost male in the *E. d. diminutus* cluster in Fig. 1). Overall, this specimen appears to be closest to *E. d. diminutus*.

Specimens of *E. diminutus* examined by me are listed below:

E. diminutus diminutus.—BRAZIL. Maranhão: Alto Parnabyba (=Parnaíba), 1♂ (FMNH). Minas Geraes: Lagoa Santa, 1♀ (alc. with skull removed) (FMNH). São Paulo: Furnas do Yporanga, 1♂ (MCZ).

E. diminutus fidelis.—ARGENTINA. Tucumán: Aguas Chiquitas, about 800 m, Sierra

de Medina, 1♂ (juvenile), 2♀, + chromosomes (CM). URUGUAY. *Rio Negro*: Arroyo Negro, 15 km S Paysandu, 1♂, 3♀ (AMNH); Quebracho Paysandu, 2♀ (FMNH).

A specimen from Itat , Corrientes, Argentina (BMNH 24.6.6.4), was not examined by me, but is referable, on the basis of measurements supplied by Mr. Hill, to *E. d. fidelis*. The specimen (BMNH 1.8.1.1) referred to *E. d. dorianus* by Davis (1966), and the specimen (UCONN 15649) assigned to *E. cf. fidelis* by Wetzel and Lovett (1974) are both *E. furinalis*. Two other specimens, which are in the Paris Museum (Museum National D'Histoire Naturelle, Register Nos. 836/631 and 838/642), and which were a part of the type series of *Vespertilio hilarii* Geoffroy, may be assignable to *E. diminutus* (see Davis, 1966:257).

ACKNOWLEDGMENTS

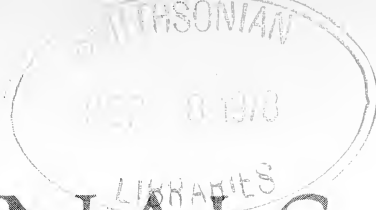
Rub n Barquez, Jorge Cajal, Tye Hafner, Ricardo Ojeda, and Connie Stuart assisted me in the field. The Miguel Lillo Instituto Superior de Ecologia of the Universidad Nacional de Tucum n furnished a vehicle for our field use. Travel expenses to Argentina were provided by California State College, Stanislaus, and by a Faculty Summer Grant from the Stanislaus State College Foundation. Suzanne Braun performed many technical and editorial chores. Mr. J. E. Hill and Dr. G. Arbocco kindly measured specimens in the British Museum of Natural History and the Museo Civico di Storia Naturale "Giacomio Doria", Genova, respectively. Drs. J. Findley, P. Freeman, K. Koopman, B. Lawrence, P. Myers, and R. Wetzel allowed me to examine specimens in their care. Dr. M. Mares permitted me to utilize an uncatalogued collection of *E. furinalis* from Crato, Brazil. Patricia Capplonch Barquez drew Figure 5. Drs. K. Koopman and W. B. Davis reviewed the manuscript and made several suggestions for improving it. I am grateful for the generous assistance of each of these persons and institutions.

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REVISION OF GENUS *MALACOMYS* OF AFRICA (MAMMALIA: MURIDAE)

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ABSTRACT

Variation in external and cranial measurements of 222 specimens of *Malacomys* was analyzed by means of univariate and multivariate statistical procedures. Significant secondary sexual variation was lacking in all measurements. Geographic samples were generally homogeneous; little individual variation was present. The data indicate that *Malacomys edwardsi* is readily separable from *M. longipes*. *Malacomys edwardsi* is considered monotypic, whereas five subspecies are recognized in *M. longipes*. The recently described *M. verschureni*, known only from the holotype, is accepted based on the description and compared with the other taxa.

INTRODUCTION

The genus *Malacomys* A. Milne-Edwards, 1877, a member of the subfamily Murinae, occurs in tropical regions of Africa. The taxonomic history of this genus has been characterized by a degree of confusion common to murine rodents. From one to four species have been recognized at various times from the eight nominal taxa that are described. Although specimens from certain parts of the range of the genus are still wanting, enough are available at this time to review the taxonomic status of the eight nominal taxa.

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The objectives of the study of this genus were to analyze nongeographic variation within at least one taxon in the genus, to analyze geographic variation within the species in the genus, and then to assess the taxonomic significance of the variation. A large sample of one taxon from a single locality was analyzed for nongeographic variation and the results were used as typical of the other, more poorly known taxa.

MATERIALS AND METHODS

A total of 222 specimens of *Malacomys* were examined; all of these were prepared as conventional museum study skins and skulls and were accompanied by standard specimen labels with appropriate data. Unless otherwise indicated, specimens examined are in the Carnegie Museum of Natural History. Others were examined from the American Museum of Natural History (AMNH) and the United States National Museum of Natural History, Smithsonian Institution (USNM).

Only adult specimens were used for statistical comparisons. These were recognized by having adult pelage, translucent auditory bullae, fused cranial sutures (particularly the basisphenoid-basioccipital suture), and wear on the occlusal surfaces on all of the molar teeth. From those specimens judged to be adults, 19 measurements were recorded in millimeters for statistical analyses. Four external measurements were recorded from specimen tags as follows: TL—total length; TA—length of tail; HF—length of hindfoot (*c.u.*); and ER—length of ear (from notch). The following cranial measurements were taken by means of dial calipers: GLS—greatest length of skull; CBL—condylobasal length of skull; GZB—greatest zygomatic breadth; LIB—least interorbital breadth; BBC—greatest breadth of braincase; GLN—greatest length of nasals; HOR—height of rostrum (taken along the vertical suture connecting premaxilla and maxilla); LAP—greatest length of anterior palatine foramina; CLT—greatest crown length of maxillary toothrow; BOP—breadth of palate (as distance between labial crown edges of M¹-M¹); LOP—length of palate (from anterior edge of premaxilla to least posterior edge of palatine); GHS—greatest height of skull (taken perpendicular to the horizontal plane of skull placed on a microscope slide); MTR—greatest crown length of mandibular toothrow; HOM—height of mandible (taken perpendicularly from ventral edge of angular process to condylar process); and LOM—length of mandible (taken from the condylar process to the posteroventral edge of alveolus of the incisor).

Localities from which specimens were examined were grouped into 14 geographical samples (OTUs) being careful not to overlap previously recognized subspecies nor obvious physiographic boundaries within the groupings. The following OTUs (identified by number) with the localities included in each group were used: 1) *SW Ivory Coast*—Duekove, Niebe, Soubre; *E Liberia*—Tars Town; 2) *S Ivory Coast*—Adiopodoume, Yapo Sud; 3) *E Ivory Coast*—Blekoum, Yabrosso; *W Ghana*—Gubinja; 4) *SW Ghana*—Efumumkrom, Prestea, Prince's Town; *SE Ivory Coast*—Ehania; 5) *S Ghana*—Abanyaso, Berekuso, Kade, Nkawkaw; 6) *S Nigeria*—Benim, Nikrowa, Sapoba; 7) *Rwanda*—Butare, Uinka; 8) *E Zaire*—Lemera; 9) *NE Zaire*—Avakubi, Gamangui, Niangara, Niapu, Medje; 10) *E Cameroon*—Batanga, Bertoua; 11) *SE Cameroon*—Bipindi, Ebolowa, Efulan, Eseka, Lolodorf, Nyabessan, Yaounde; 12) *W Cameroon*—Mamfe; 13) *SW Ghana*—Ankasa River Forest Reserve, Ghiriso; and 14) *Central Zaire*—Luluabourg.

It was not possible at this time to examine any specimens deposited in museums in Europe or Africa; thus none of the holotypes have been studied nor have all of the extant specimens been examined. Furthermore, we have not examined any specimens of *M. l. australis* (known only from Zambia), any adult skulls of *M. l. giganteus*, nor the recently described *M. verschureni* Verheyen and Van Der Straeten, 1977.

Univariate statistical analyses of individual and secondary sexual variations were performed by a program called UNIVAR (Powers, 1970). This program yields, among others, the following standard univariate statistics: mean; standard error of mean; standard deviation; variance; range; coefficient of variation. In addition, UNIVAR performs the Sum of Squares Simultaneous Test Procedure (SS-STP) when two or more groups are compared. This procedure determines the maximally nonsignificant differences.

Additionally, multivariate statistical analyses were performed using selected subroutines of the NT-SYS program developed at the University of Kansas by F. J. Rohlf, R. Bartcher, and J. Kishpaugh. The NT-SYS program computes a matrix of Pearson's correlation coefficients and a matrix of phenetic distance coefficients from standardized character values. Cluster analyses were generated using UPGMA (unweighted pair-group method using arithmetic averages) on the correlation and distance matrices. Phenograms were generated from each matrix. The coefficient of cophenetic correlation is given to show the goodness of fit between the phenograms and the original matrices. From the correlation matrix, the first three principal components (PCA) were extracted and a three-dimensional projection was made onto the first three principal components with the results plotted in the projection figure. The percentage of variation accounted for in each component is given. The character loadings of each component are listed.

Finally, Kruskal's nonmetric multidimensional scaling analysis was performed as part of the MDSCALE subroutine of NT-SYS using the distance matrix. This analysis shows more accurately the differences between close OTUs as seen in the principal component analysis, minimizes stress between the configuration of points in the multidimensional space and the original distance matrix, and is preferred if there are a small number of OTUs (Rohlf, 1972). These results are plotted as a three-dimensional projection with the points connected by a single linkage cluster matrix or minimum spanning tree (Prim-Network of Prim, 1957) for interpoint similarity. A stress value indicates the degree of reliability that the original multidimensional distance matrix is represented in the three-dimensional projection. The lower the stress value, the better is the representation.

Differences in color of pelage originally were considered as a possible quantitative character but had to be discarded because of small samples and the influence of wear and molt on the pelage, conditions of skins, and the number of years some specimens had been in museums.

TAXONOMIC HISTORY

The genus *Malacomys* was proposed by A. Milne-Edwards (1877:9) for material from the Gaboon [=Gabon] River in Gabon, with the newly described *M. longipes* A. Milne-Edwards, 1877, as type species. The first four proposed nominal taxa in the genus were described as full species (*M. longipes* A. Milne-Edwards, 1877; *M. edwardsi* De Rochebrune, 1885; *M. centralis* De Winton, 1897; and *M. wilsoni* Thomas, 1916).

In the first review of the genus, Hayman (1936) retained two species—*M. edwardsi* for specimens from Liberia to Nigeria and *M. longipes* for those from Cameroon and "Congo basin east to Ruwenzori and south to the Kasai area." Hayman further placed as subspecies of *M. longipes* the nominal taxa *M. centralis* and *M. wilsoni*. However, Allen (1939) listed all four taxa as full species. Following Hayman's treatment of the genus, Ellerman (1941) retained two species with *M. longipes* having two additional subspecies.

In their reclassification of southern African mammals, Ellerman et al. (1953) inferred that there was only one species in the genus *Malacomys* by giving the distribution for *M. longipes* as extending as far as Liberia even though this area had been previously included only within the geographic range of *M. edwardsi*. Subsequently Heim de Balsac and Lamotte (1958) placed *M. edwardsi* as a subspecies of *M. longipes* in their report on rodents from Mt. Nimba. But in describing two new subspecies of *M. longipes*, Ansell (1958) questioned the fact that *M. longipes* and *M. edwardsi* could be conspecific because *M. l. cansdalei* occurred in an area previously thought to contain only *M. edwardsi*. But he deferred any final judgement until more material was available to determine whether *M. edwardsi* and *M. l. cansdalei* were allopatric in this area. However, Heim de Balsac and Aellen (1965) continued to regard *M. edwardsi* as a subspecies of *M. longipes*. The former was considered to be merely the West African representative of the species.

With some hesitation, Bellier and Gautun (1968) published the description of a new subspecies of *Malacomys longipes* from southern Ivory Coast. These authors stated that if their new subspecies, *M. l. giganteus*, proved to be valid, then *M. edwardsi* must be recognized as a valid species due to the sympatry of the two taxa in southern Ivory Coast.

Rosevear (1969), after examining the western African specimens of *Malacomys* in the British Museum, recognized both *M. edwardsi* and *M. longipes* as distinct species, but expressed some doubt about his conclusion because of inadequate material to clarify the taxonomic status of the two species in Ghana. But both *M. edwardsi* and *M. l. cansdalei* were available from Ankasa River Forest Reserve. Further, he felt, based on six specimens, that *M. l. cansdalei* differed markedly, especially in length of hindfoot and ear, from *M. longipes* of Cameroon, was separated from it widely geographically, and might even be a distinct species.

The taxonomic relationships of western African *Malacomys* was clarified further by Cole (1972:616) when he reported sympatry between *M. longipes cansdalei* and *M. edwardsi* in southern Ghana. Based upon Student's *t*-test, significant differences were found between population samples of *M. l. cansdalei* and *M. edwardsi* from Ghana. Cole (1972:616) felt that *M. l. cansdalei* was best left as a subspecies of *M. longipes* in spite of Rosevear's (1969) reservation on the subject.

Misonne (1974) listed two species, *M. longipes* and *M. edwardsi*, and inferred possible sympatry in the distribution of the two species in Ivory Coast and Ghana.

More recently, Verheyen and Van Der Straeten (1977) described a

new species of *Malacomys* from eastern Zaire. This new species, *M. verschureni*, is characterized by having six plantar tubercles and being small for the genus, similar in size to *M. edwardsi*.

RESULTS AND DISCUSSION

Nongeographic Variation

Due to small sample sizes of subadults, variation with age could not be analyzed. For the analyses of individual and secondary sexual variations, only adults were used.

Secondary sexual variation.—A geographic sample of each sex of *M. longipes* from Gamangui, northeastern Zaire, was used to test for secondary sexual variation. The results of the single classification ANOVA performed are given in Table 1.

The results reveal that males averaged larger than females in 11 of 19 variables analyzed and females averaged larger than males in three measurements. However, there was no statistically significant difference between means of either sex in any of the 19 variables at the 0.05 level of significance. Based upon these results of tests for significant secondary sexual dimorphism and the apparent lack of such dimorphism in *M. longipes*, the data for both sexes were combined for the multivariate statistical analysis of all samples of the genus.

Individual variation.—Individual variation as indicated by the coefficient of variation was found to be low in both sexes in the sample of *Malacomys longipes* from Gamangui, Zaire (Table 1). Only three of 38 measurements by sex had coefficients of variation greater than 6.00, whereas 29 of the measurements has values less than 5.00. Coefficients of variation of less than 6.00 are within the limits of those generally found for other small rodents (Genoways, 1973). Length of tail in males and length of anterior palatine foramina and height of mandible in females were the only variables with coefficients of variation over 6.00. Even the external measurements, particularly the length of hindfoot and ear, in this series of specimens had low coefficients of variation. These low values may be ascribed to the fact that this series of specimens was collected and measured in the field by only one person over a relatively short period of time.

Additional coefficients of variation were obtained in the analysis of geographic variation (Table 2). Of the four external measurements tested for 12 geographic samples, three samples (OTUs 2, 4, and 7) had coefficients of variation greater than 6.00 for total length; six samples (OTUs 2, 4, 5, 9, 10, and 13) for length of tail, three samples (OTUs 10, 11, and 13) for length of hindfoot, and five samples (OTUs 1, 4, 5, 10, and 11) for length of ear. For cranial variables, only five had coefficients of variation over 6.00—greatest length of nasals,

Table 1.—*Secondary sexual variation in 19 external and cranial measurements of Malacomys longipes from Gamangui, Zaire. Abbreviations for standard univariate statistics are as follows: N = sample size; 2SE = two standard errors of the mean; Minimum = minimum value of range; Maximum = maximum value of range; and CV = coefficient of variation; those for measurements are given in materials and methods section of text. Single classification ANOVA (F-test with significant level of 0.05) indicated no significant differences between means of sexes.*

Measurement and sex	N	Mean	2 SE	Minimum	Maximum	CV
TL						
Male	13	347.8	10.65	313.0	371.0	5.52
Female	9	350.0	9.94	327.0	372.0	4.26
TA						
Male	13	187.2	6.44	171.0	206.0	6.20
Female	9	190.2	4.73	179.0	203.0	3.73
HF						
Male	13	40.77	0.61	38.0	42.0	2.68
Female	9	40.67	0.47	40.0	42.0	1.74
ER						
Male	13	29.2	0.44	28.0	30.0	2.75
Female	9	28.7	0.47	28.0	30.0	2.47
GLS						
Male	12	41.8	0.98	39.0	44.7	4.07
Female	9	41.5	0.75	39.7	43.1	2.70
CBL						
Male	12	38.7	0.95	35.6	41.0	4.25
Female	7	38.4	0.71	36.8	39.3	2.44
GZB						
Male	12	17.7	0.44	16.2	18.6	4.34
Female	9	17.8	0.36	17.0	18.6	3.01
LIB						
Male	12	6.9	0.14	6.5	7.3	3.54
Female	9	6.8	0.18	6.2	7.1	3.96
BBC						
Male	12	13.9	0.19	13.3	14.3	2.35
Female	9	13.8	0.18	13.4	14.2	1.91
GLN						
Male	12	16.4	0.52	14.9	18.1	5.46
Female	9	16.4	0.56	15.0	17.7	5.16
HOR						
Male	12	7.7	0.24	7.0	8.3	5.30
Female	9	7.7	0.22	7.2	8.2	4.27
LAP						
Male	12	5.9	0.14	5.4	6.2	4.09
Female	9	5.9	0.28	5.4	6.6	7.15

Table 1.—(Continued)

Measurement and sex	N	Mean	2 SE	Minimum	Maximum	CV
CLT						
Male	12	5.8	0.11	5.5	6.0	3.19
Female	8	5.7	0.12	5.5	6.0	3.09
BOP						
Male	12	7.6	0.18	7.0	8.0	4.16
Female	8	7.5	0.09	7.3	7.7	1.66
LOP						
Male	12	21.5	0.51	20.2	22.7	4.09
Female	9	21.1	0.42	20.2	22.2	2.99
GHS						
Male	10	13.2	0.38	12.3	14.1	4.54
Female	8	13.1	0.40	12.1	13.7	4.34
MTR						
Male	10	5.6	0.10	5.4	5.9	2.17
Female	9	5.6	0.08	5.5	5.9	2.17
HOM						
Male	12	10.4	0.33	9.4	11.1	5.46
Female	9	10.4	0.44	9.5	11.1	6.37
LOM						
Male	12	21.0	0.62	19.5	23.0	5.14
Female	9	20.9	0.62	19.3	22.0	4.46

height of rostrum, greatest length of anterior palatine foramina, height of mandible and length of mandible. Four samples (OTUs 2, 7, 9, and 13) were over the value of 6.00 for length of nasals. Only one sample, OTU 2, was high for height of rostrum. Length of anterior palatine foramina exhibited the most individual variation of all variables tested. For this variable, geographic samples 1, 2, 3, 7, 8, 9, 11, 13, and 14 had coefficients of variation over 6.00. Four samples, OTUs 1, 2, 7, and 11, had values over 6.00 for height of mandible. Sample 2 had a value over 6.00 for length of mandible. Highest coefficients of variation, 13.2, were found for length of nasals for sample 7 and for height of mandible for sample 11.

Of the 15 cranial variables tested for the 12 geographic samples, a total of 144 samples of cranial measurements of the possible 180 samples had coefficients of variation of less than 5.00. Cranial measurements showing especially low values for all geographic samples were least interorbital breadth, breadth of braincase, crown length of maxillary toothrow, height of skull, and crown length of mandibular toothrow.

Table 2.—*Geographic variation in external and cranial measurements of five samples (numbers 1–5) of combined sexes of Malacomys edwardsi and seven samples (numbers 7–11, 13, and 14) of combined sexes of M. longipes. See text for key to sample numbers and definitions of measurements.*

Sample number	N	Mean	Range	2 SE	CV
Total length					
1	16	319.1	296–357	8.24	5.17
2	6	304.8	283–348	19.39	7.79
3	9	311.1	301–319	3.49	1.68
4	8	308.6	283–334	16.63	6.25
5	18	303.4	283–331	7.00	4.89
7	6	314.5	270–340	20.40	7.94
8	12	323.0	302–342	7.96	4.27
9	36	347.3	300–375	5.99	5.17
10	7	324.4	302–346	11.64	4.74
11	15	329.1	309–346	5.65	3.33
13	13	329.6	292–353	9.80	5.36
14	7	351.0	332–388	14.30	5.39
Length of tail					
1	16	175.8	159–191	4.99	5.67
2	6	166.3	157–193	11.06	8.14
3	9	171.6	160–183	5.37	4.69
4	8	167.1	151–183	8.90	7.53
5	18	160.9	143–180	4.91	6.48
7	6	170.8	155–186	8.33	5.97
8	12	173.5	162–182	3.01	3.01
9	36	185.1	134–206	4.74	7.69
10	7	175.6	160–195	9.27	6.94
11	15	173.2	161–190	4.19	4.68
13	13	189.0	157–206	8.43	8.04
14	7	192.1	181–214	8.55	5.88
Length of hindfoot					
1	16	35.4	32–37	0.68	3.84
2	6	35.8	35–37	0.61	2.10
3	9	33.4	32–35	0.59	2.64
4	8	34.8	33–38	1.18	4.80
5	17	33.5	31–35	0.57	3.52
7	6	38.5	38–40	0.68	2.17
8	12	37.1	35–39	0.72	3.34
9	35	40.9	38–44	0.35	2.50
10	7	36.6	30–41	2.58	9.32
11	15	35.9	26–40	1.73	9.32
13	13	41.1	33–44	1.86	8.16
14	8	37.8	35–41	1.45	5.44
Length of ear					
1	14	28.3	21–31	1.33	8.82
2	5	26.6	25–28	1.02	4.29
3	9	26.1	24–29	0.97	5.56
4	8	27.1	25–31	1.33	6.95

Table 2.—(Continued)

Sample number	N	Mean	Range	2 SE	CV
5	17	27.0	24–31	1.07	8.18
7	6	26.0	25–27	0.73	3.44
8	12	27.3	25–30	0.93	5.88
9	35	28.1	24–30	0.53	5.53
10	5	24.6	23–28	1.85	8.43
11	14	23.6	18–25	1.10	8.72
13	13	28.4	27–31	0.58	3.68
14	6	27.8	26–30	1.31	5.76
Greatest length of skull					
1	5	36.6	35.4–37.8	0.77	2.35
2	5	37.2	34.9–40.2	1.86	5.60
3	7	37.3	35.8–38.5	0.71	2.51
4	8	37.4	35.3–38.8	0.87	3.28
5	16	38.0	35.9–40.3	0.57	2.98
7	5	41.1	37.4–42.5	1.88	5.12
8	12	41.4	39.3–42.8	0.67	2.82
9	33	41.8	39.0–44.7	0.47	3.25
10	5	40.2	38.7–41.5	0.91	2.54
11	7	40.8	38.0–42.4	1.05	3.47
13	10	40.0	38.5–41.8	0.67	2.63
14	12	41.6	39.9–44.5	0.84	3.48
Condylobasal length of skull					
1	5	34.1	32.4–35.6	1.27	4.15
2	5	33.9	31.9–36.7	1.70	5.64
3	7	34.0	32.4–34.9	0.74	2.88
4	8	34.0	32.2–35.9	0.92	3.81
5	16	34.6	33.0–36.5	0.55	3.18
7	5	38.0	34.4–39.7	1.91	5.62
8	12	37.8	36.1–39.7	0.63	2.87
9	31	38.6	35.6–41.0	0.48	3.43
10	4	36.1	34.5–37.9	1.66	4.59
11	8	37.2	34.8–39.5	1.05	4.02
13	10	36.1	35.1–37.4	0.54	2.34
14	12	38.0	36.5–40.3	0.71	3.25
Zygomatic breadth					
1	6	15.1	14.2–15.6	0.46	3.70
2	6	14.7	13.5–15.6	0.64	5.32
3	7	15.2	14.7–16.2	0.39	3.40
4	8	15.0	14.3–15.7	0.35	3.26
5	17	15.4	14.6–16.2	0.24	3.21
7	6	17.5	16.4–18.0	0.49	3.45
8	11	18.0	17.1–18.7	0.28	2.54
9	32	17.9	16.2–19.0	0.23	3.70
10	6	17.0	15.9–18.2	0.68	4.88
11	11	17.1	15.4–19.0	0.59	5.73
13	11	16.3	15.4–17.5	0.43	4.40
14	12	17.8	16.9–18.8	0.31	3.01

Table 2.—(Continued)

Sample number	N	Mean	Range	2 SE	CV
Least interorbital breadth					
1	6	5.5	5.2–5.9	0.20	4.45
2	6	5.6	5.2–6.0	0.22	4.79
3	7	5.4	5.3–5.6	0.07	1.79
4	8	5.5	5.3–5.7	0.12	2.98
5	18	5.5	5.1–5.9	0.10	3.71
7	6	6.7	6.6–6.9	0.08	1.53
8	12	7.1	6.4–7.5	0.18	4.45
9	35	6.8	6.2–7.5	0.10	4.47
10	6	6.5	6.1–7.0	0.25	4.66
11	13	6.6	6.2–7.0	0.12	3.18
13	11	6.0	5.8–6.3	0.12	3.27
14	12	6.6	6.1–7.2	0.18	4.77
Height of rostrum					
1	6	6.3	6.0–6.5	0.17	3.25
2	6	6.5	6.0–7.0	0.36	6.68
3	7	6.3	6.1–6.6	0.15	3.15
4	8	6.6	6.2–6.9	0.16	3.40
5	18	6.8	6.4–7.2	0.10	3.14
7	6	7.5	6.9–7.8	0.27	4.46
8	13	7.6	7.1–7.9	0.16	3.88
9	35	7.7	6.7–8.4	0.13	5.01
10	6	7.5	6.9–8.2	0.35	5.66
11	15	7.5	6.9–8.1	0.20	5.18
13	12	7.3	6.5–7.7	0.20	4.77
14	12	7.9	7.2–8.6	0.26	5.70
Length of anterior palatine foramina					
1	6	6.5	5.3–7.4	0.56	10.48
2	6	6.6	5.8–7.3	0.42	7.85
3	7	6.2	4.9–6.9	0.50	10.62
4	8	6.4	6.1–6.7	0.15	3.26
5	18	6.5	5.7–7.1	0.16	5.33
7	6	5.7	5.1–6.3	0.32	6.94
8	13	5.8	5.0–6.3	0.24	7.42
9	35	6.0	5.1–6.8	0.12	6.05
10	6	6.0	5.8–6.7	0.28	5.80
11	15	5.7	5.0–6.5	0.21	6.99
13	12	6.2	5.4–6.9	0.25	7.06
14	12	5.7	5.0–6.8	0.32	9.55
Breadth of braincase					
1	6	13.5	12.5–14.3	0.49	4.47
2	5	13.2	12.9–13.6	0.29	2.47
3	7	13.2	12.7–13.6	0.21	2.13
4	8	13.4	12.9–14.1	0.37	3.88
5	16	13.4	12.8–13.8	0.15	2.18

Table 2.—(Continued)

Sample number	N	Mean	Range	2 SE	CV
7	5	14.1	13.4–14.3	0.34	2.69
8	12	13.9	13.6–14.4	0.15	1.92
9	34	13.9	13.2–15.1	0.14	2.85
10	6	14.1	13.8–14.9	0.36	3.11
11	11	13.8	13.2–14.7	0.22	2.68
13	10	14.5	14.0–15.2	0.28	3.02
14	12	14.1	13.0–14.7	0.29	3.60
Length of nasals					
1	6	14.6	14.2–15.1	0.28	2.35
2	6	15.1	13.5–16.8	1.02	8.32
3	7	14.9	13.7–15.9	0.57	5.06
4	8	15.0	14.0–15.9	0.43	4.05
5	18	15.4	14.3–16.6	0.34	4.63
7	6	15.6	12.3–17.3	1.68	13.16
8	13	16.5	15.4–19.9	0.67	7.38
9	35	16.5	14.9–18.1	0.28	5.07
10	6	16.2	15.2–16.8	0.50	3.78
11	14	16.5	14.5–17.8	0.51	5.76
13	12	15.7	14.0–18.9	0.67	7.43
14	12	16.6	15.4–17.7	0.44	4.58
Crown length of maxillary toothrow					
1	6	4.8	4.7–4.9	0.06	1.56
2	6	4.7	4.6–4.9	0.10	2.49
3	7	4.6	4.1–4.8	0.18	5.33
4	8	4.7	4.5–4.9	0.10	2.88
5	18	4.7	4.4–4.9	0.06	2.78
7	6	5.5	5.4–5.6	0.06	1.36
8	13	5.5	5.2–5.8	0.10	3.30
9	33	5.7	5.4–6.0	0.06	2.97
10	6	5.4	5.0–5.7	0.21	4.68
11	15	5.5	5.1–5.9	0.11	3.91
13	12	5.2	4.8–5.4	0.12	4.01
14	10	5.8	5.6–6.0	0.08	2.28
Breadth of palate					
1	5	6.7	6.4–7.0	0.19	3.23
2	6	6.8	6.4–7.4	0.31	5.68
3	7	6.7	6.4–7.1	0.20	3.96
4	8	6.8	6.6–7.0	0.10	2.20
5	18	6.8	6.4–7.2	0.10	3.27
7	6	7.4	7.3–7.6	0.10	1.58
8	13	7.6	7.1–7.8	0.13	3.04
9	33	7.6	7.0–8.0	0.08	3.13
10	6	7.1	6.8–7.5	0.23	3.92
11	14	7.2	6.6–7.8	0.16	4.04
13	12	7.4	6.8–8.1	0.22	5.14
14	10	7.7	7.3–8.3	0.19	3.85

Table 2.—(Continued)

Sample number	N	Mean	Range	2 SE	CV
Length of palate					
1	6	18.6	17.4–19.8	0.78	5.11
2	6	18.4	17.4–19.6	0.81	5.39
3	7	18.1	17.2–18.7	0.45	3.26
4	8	18.2	17.3–19.1	0.42	3.28
5	18	18.5	17.4–19.4	0.24	2.80
7	6	21.1	19.2–21.7	0.78	4.53
8	12	21.0	19.8–22.2	0.38	3.15
9	35	21.4	19.8–22.7	0.26	3.60
10	6	20.3	19.9–20.6	0.20	1.20
11	14	20.9	19.2–22.7	0.54	4.82
13	12	19.2	18.1–20.1	0.37	3.30
14	12	21.1	20.0–22.4	0.42	3.45
Height of skull					
1	5	11.3	10.7–11.8	0.40	3.97
2	5	11.3	10.8–11.8	0.38	3.75
3	7	11.4	11.0–11.6	0.17	1.96
4	8	11.4	11.2–11.7	0.12	1.44
5	15	11.6	11.2–12.2	0.16	2.62
7	5	12.7	11.9–13.1	0.43	3.82
8	12	13.5	12.4–14.5	0.36	4.56
9	28	13.1	12.1–14.1	0.19	3.78
10	5	12.7	12.2–14.0	0.68	5.96
11	9	12.4	11.7–13.1	0.30	3.57
13	10	12.9	12.2–13.6	0.28	3.47
14	11	13.2	12.7–13.9	0.22	2.83
Crown length of mandibular tooththrow					
1	6	4.7	4.5–4.9	0.11	2.89
2	6	4.8	4.7–4.8	0.04	1.15
3	7	4.6	4.2–4.8	0.14	4.17
4	8	4.7	4.6–4.9	0.08	2.47
5	18	4.6	4.3–4.8	0.07	3.11
7	6	5.5	5.3–5.7	0.12	2.72
8	13	5.6	5.2–5.8	0.11	3.56
9	33	5.6	5.2–6.0	0.06	2.94
10	6	5.4	5.1–5.5	0.12	2.81
11	16	5.4	5.2–5.7	0.08	3.05
13	12	5.7	4.7–5.5	0.12	3.90
14	11	5.7	5.5–5.9	0.08	2.29
Height of mandible					
1	6	7.9	6.7–8.7	0.60	9.27
2	6	7.9	7.1–8.7	0.51	7.90
3	7	8.3	7.9–8.7	0.25	3.93
4	8	8.1	7.2–8.6	0.32	5.57
5	18	8.2	7.3–9.0	0.23	5.88
7	6	10.0	8.5–10.5	0.61	7.51
8	13	10.4	9.8–11.2	0.27	4.61

Table 2.—(Continued)

Sample number	N	Mean	Range	2 SE	CV
9	35	10.4	9.0–11.3	0.21	5.85
10	6	9.6	9.1–9.8	0.21	2.71
11	15	9.1	5.9–11.2	0.62	13.17
13	12	8.4	7.7–9.3	0.26	5.46
14	12	10.0	9.1–10.8	0.31	5.33
Length of mandible					
1	6	18.1	16.6–18.6	0.62	4.23
2	6	18.1	16.6–19.6	0.90	6.06
3	7	18.4	17.1–19.6	0.74	5.30
4	8	17.8	16.9–18.8	0.49	3.86
5	18	18.3	16.9–19.6	0.33	3.84
7	6	20.9	19.0–21.8	0.82	4.82
8	13	21.1	19.7–21.9	0.37	3.20
9	35	21.0	19.1–23.0	0.32	4.53
10	6	20.0	19.2–20.8	0.53	3.23
11	15	20.0	18.5–22.1	0.50	4.80
13	12	19.2	18.1–20.3	0.37	3.30
14	12	20.9	19.5–22.7	0.48	3.97

Geographic Variation

Specimens of the nominal taxa of *Malacomys* were grouped into 14 geographic samples (OTUs) for the analysis of geographic variation (Figs. 1–3). Of these 14 samples, all but two samples (OTUs 6 and 12) had a sufficiently large number of individuals, at least three, of each variable to be entered in the Sum of Squares Simultaneous Test Procedure (SS-STP) to determine the maximally nonsignificant subsets between and among means of each variable for the geographic samples. Table 2 gives standard statistics for the 19 variables from the 12 geographic samples. Table 3 gives a series of means with maximally nonsignificant subsets for ten selected external and cranial measurements in order to demonstrate trends in geographic variation. Fig. 1 gives a graphic representation of these same trends for six measurements.

Results of these univariate analyses of geographic variation (Table 2 and 3, Fig. 1) indicate that OTUs 1 to 5 are characterized by small size with little variation between samples. Samples 7 to 11 and 13 to 14 are characterized by large size and exhibit more variation among the samples. In most instances, OTUs 7, 8, 9, and 14 are grouped together as one subset characterized by large size. OTUs 10 and 11 are grouped together as another subset, generally characterized by intermediate size. OTU 13 is a variable sample, being intermediate in size for some measurements and large for others.

Table 3.—Results of 10 typical SS-STP analyses of geographic variation in *Malacomys edwardsi* (samples 1–5) and *M. longipes* (samples 7–11, 13, and 14). Vertical lines to the right of each series of means connect maximally nonsignificant subsets at the 0.05 level of significance. See Figs. 2 and 3 and text for key to geographic samples included in each sample number.

<i>Total length</i>			<i>Length of hindfoot</i>		
Sample number	Means	Results SS-STP	Sample number	Means	Results SS-STP
14	351.0		13	41.1	
9	347.3		9	40.9	
13	329.6		7	38.5	
11	329.1		14	37.8	
10	324.4		8	37.1	
8	323.0		10	36.6	
1	319.1		11	35.9	
7	314.5		2	35.8	
3	311.1		1	35.4	
4	308.6		4	34.8	
2	304.8		5	33.5	
5	303.4		3	33.4	
<i>Greatest length of skull</i>			<i>Greatest zygomatic breadth</i>		
Sample number	Means	Results SS-STP	Sample number	Means	Results SS-STP
9	41.8		8	18.0	
14	41.6		9	17.9	
8	41.4		14	17.8	
7	41.1		7	17.5	
11	40.8		11	17.1	
10	40.2		10	17.0	
13	40.0		13	16.3	
5	38.0		5	15.4	
4	37.4		3	15.2	
3	37.3		1	15.1	
2	37.2		4	15.0	
1	36.6		2	14.7	
<i>Least interorbital breadth</i>			<i>Greatest breadth of braincase</i>		
Sample number	Means	Results SS-STP	Sample number	Means	Results SS-STP
8	7.1		13	14.5	
9	6.8		10	14.1	
7	6.7		14	14.1	
14	6.6		7	14.1	
11	6.6		8	13.9	
10	6.5		9	13.9	
13	6.0		11	13.8	
2	5.6		1	13.5	
5	5.5		4	13.4	
4	5.5		5	13.4	
1	5.5		3	13.2	
3	5.4		2	13.2	

Table 3.—(Continued)

Greatest length of anterior palatine foramina			Greatest crown length of maxillary tooththrow		
Sample number	Means	Results SS-STP	Sample number	Means	Results SS-STP
2	6.6		14	5.8	
5	6.5		9	5.7	
1	6.5		7	5.5	
4	6.3		8	5.5	
13	6.2		11	5.5	
3	6.2		10	5.4	
10	6.0		13	5.2	
9	6.0		1	4.8	
8	5.8		2	4.7	
14	5.8		4	4.7	
11	5.8		5	4.7	
7	5.7		3	4.6	

Length of palate			Greatest crown length of mandibular tooththrow		
Sample number	Means	Results SS-STP	Sample number	Means	Results SS-STP
9	21.4		14	5.7	
7	21.1		9	5.6	
14	21.1		8	5.6	
8	21.0		7	5.5	
11	21.0		11	5.4	
10	20.3		10	5.4	
13	19.2		13	5.2	
1	18.6		2	4.8	
5	18.5		1	4.7	
2	18.4		4	4.7	
4	18.2		5	4.6	
3	18.1		3	4.6	

Patterns of geographic variation indicate that the samples exhibiting small size (OTUs 1–5) are not variable geographically. These OTUs represent *Malacomys edwardsi*, and, judging by the results of the univariate analysis, this species must be considered as monotypic. Noteworthy is the abrupt separation of the samples representing this species (OTUs 1–5) from the other samples in the variables of greatest length of skull, least interorbital breadth, and crown lengths of both upper and lower tooththrows. On the other hand, these same samples of *M. edwardsi* average larger than most of the remaining samples for the length of anterior palatine foramina. Thus the relative length of the anterior palatine foramina to the length of skull in *M. edwardsi* is large for the genus.

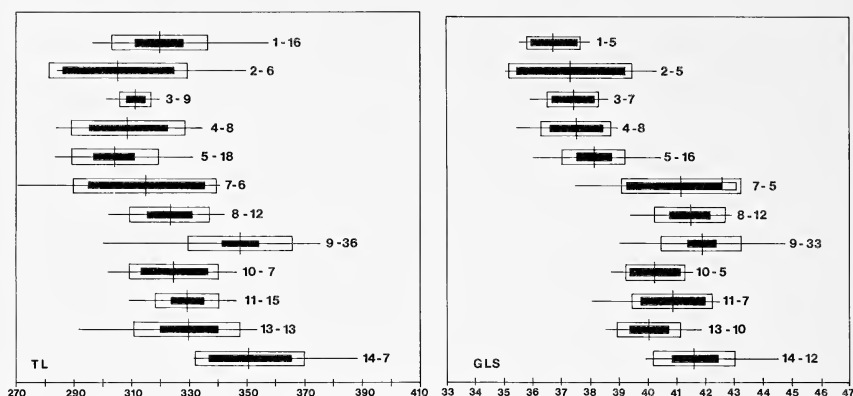


Fig. 1.—Dice grams for six selected external and cranial measurements of 12 geographic samples (OTUs) of combined sexes of *Malacomys edwardsi* and *M. longipes*. The horizontal line represents range, vertical line the mean, open rectangle one standard deviation, and closed rectangle two standard errors of the mean. The first number to the right of the grams is the sample number, the second is the sample size. See Figs. 2 and 3 and text for key to samples and definition of measurements.

Significant differences between the means of the samples 7 to 11 and 13 to 14 are present. Patterns of geographic variation indicate that the eastern samples (OTUs 7, 8, 9, and 14) are large for this group of samples for measurements of length of skull; measurements of skull breadth except braincase but including the breadth of palate; measurements of toothrow length; and for all dimensions of the mandible. These eastern samples are medium for the group for the length of hindfoot and small for the length of anterior palatine foramina.

The samples from the Cameroon show patterns of geographic variation indicating a general medium size for most measurements, especially those reflecting skull length and width, lengths of toothrow, and dimensions of the mandible. Small size for the group is suggested by the external measurements of hindfoot and ear as well as the cranial dimension of width of palate.

Large size is shown for the sample from Ghana (OTU 13) for the external measurements of hindfoot and ear. For cranial dimensions, a bulbous cranium is reflected by the large size of the mean for breadth of braincase for the Ghanaian sample, which otherwise is characterized by narrow dimensions for the other measurements reflecting skull width. Additionally, this sample exhibits long anterior palatine foramina. For the group, the Ghanaian sample has medium dimensions for the breadth of palate. Measurements for the lengths of the skull, toothrows, and dimensions of the mandible are small for the sample from Ghana relative to the whole group.

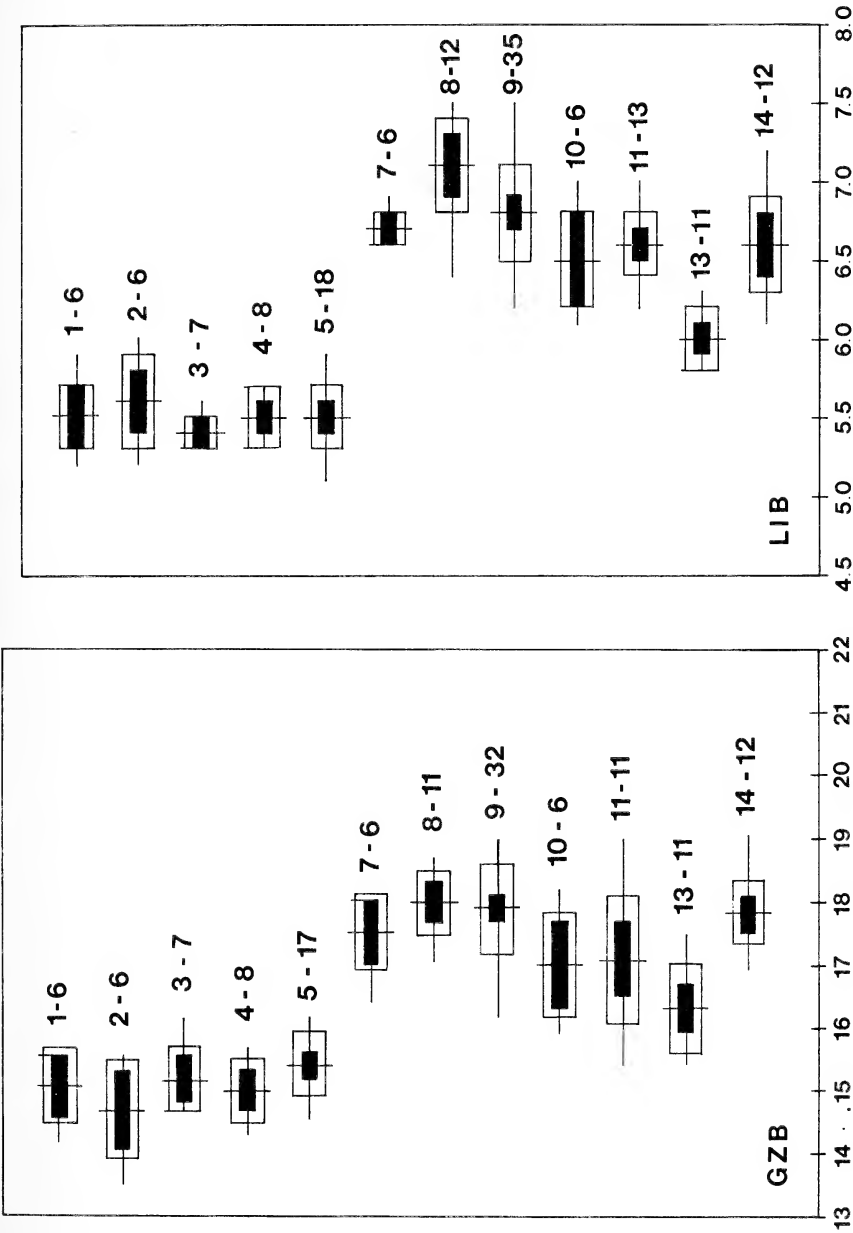


Fig. 1.—(Continued)

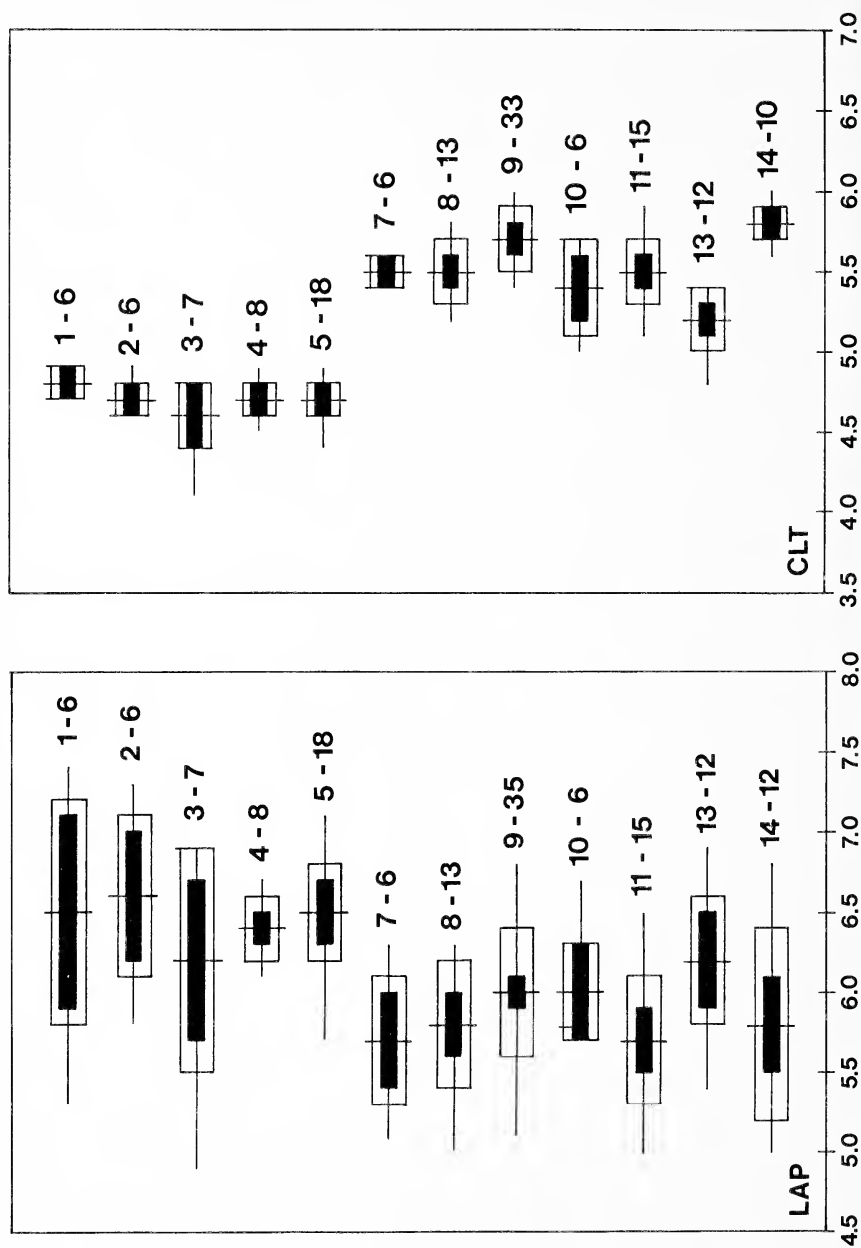


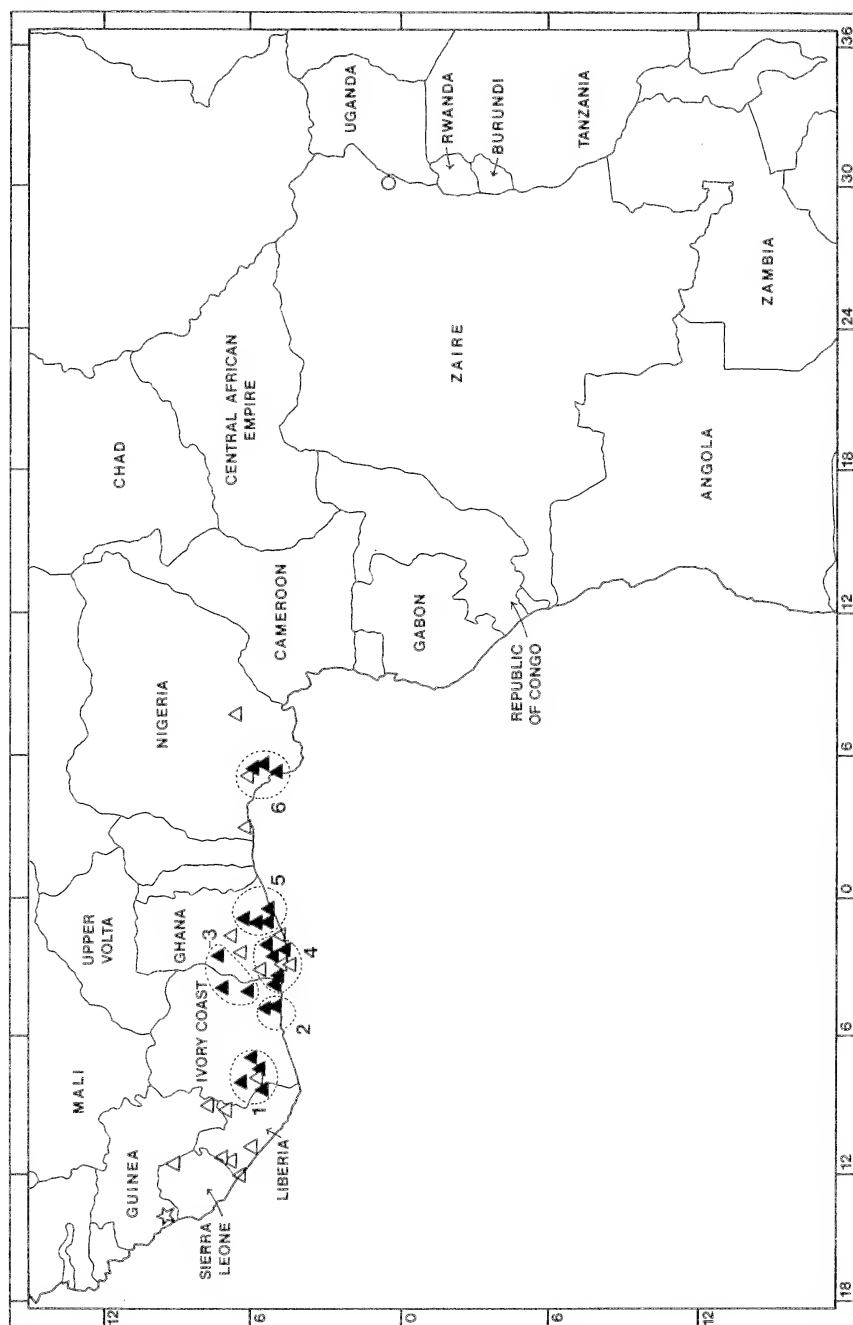
Fig. 1.—(Continued)

Means for each of the 14 geographic samples for the four external and 15 cranial measurements were used in the NT-SYS multivariate analysis. Phenograms diagramming the phenetic relationships were computed by cluster analysis from both distance and correlation matrices. The phenogram based on the distance matrix is shown in Fig. 4. The coefficient of cophenetic correlation for the distance phenogram is 0.846. The geographic samples in this phenogram are divided into two major clusters. Samples 1–6 are distantly separated in the first cluster by a phenetic distance of 1.70. In the second cluster there are at least three subclusters. The first subcluster consists of four samples (7, 8, 9, and 14) and the second contains three samples (10, 11, and 12). The third subcluster has the single sample 13.

Fig. 5 indicates the distance coefficients between the connected samples (OTUs) as drawn from Figs. 2 and 3. In most cases, for ease of diagrammatic presentation, only the distance coefficient for adjacent samples have been given. The largest distance coefficients were found between sample 13 and the adjacent samples (2, 3, 4, and 5); only the lowest of these (1.482 between 5 and 13) is plotted. The distance coefficient between samples 13 and 6 is equally high at 1.253. Distance coefficients of more than 1.00 were generated between the central African samples (9 and 14) and the Cameroon samples (10 and 11). It is interesting to note that the distance coefficient between samples 12 and 13 is 1.178, whereas that between 12 and 6 is only 0.814. Distance coefficients between samples 1 through 6 were less than 0.650. Central African localities (7, 8, 9, and 14) were characterized by distance coefficients of between 0.417 (the lowest plotted) and 0.961.

The first three principal components as computed from the matrix of correlation among the 19 variables is shown in a three-dimensional projection in Fig. 6. The first principal component expresses 76.03% of the phenetic variation, the second 10.72%, and the third 4.04% for a combined expression of 90.97% of the phenetic variation. From the results of the factor analyses (Table 4), it appears that both external and cranial measurements, but particularly the latter, had a strong effect on the first component. Specimens that were smallest overall are positioned to the left; samples are then arranged in ascending order relative to size, with the largest individuals on the right.

Character loadings (Table 4) on the second component consist primarily of the length of ear and to a lesser degree, the lengths of tail, hindfoot, and anterior palatine foramina. Samples with higher dimensions for these measurements are positioned near the bottom of the projection plot. Factor analysis indicates that the third component is influenced by high negative values for breadth of braincase and length of tail and by high positive values for the anterior palatine foramina



and height of mandible. Samples 12 and 13 separate most from the other samples on the third component.

The three-dimensional projection plot of the nonmetric multidimensional scaling analysis (MDSAL) for the 14 geographic sample means is shown in Fig. 7. Lines connecting the circles indicate the single minimum spanning tree. Stress for this projection is 0.021; a low figure indicating a good representation of the distance matrix in the three-dimensional plot.

The same results were seen in the MDSAL analysis as shown in Fig. 7 as were found in the PCA analysis (Fig. 6). Samples 1–6 are separated as one group on the left of the projection. Samples 7, 8, 14, and 9 are connected in a linear fashion, whereas samples 11 and 12 are linked to sample 10. Sample 12 also serves to connect the group on the left (samples 1 to 6) with the remaining samples. The western African sample 13 is linked to sample 10 rather than to any of its neighboring samples (1 to 6) nor to its nearest Cameroon sample (12).

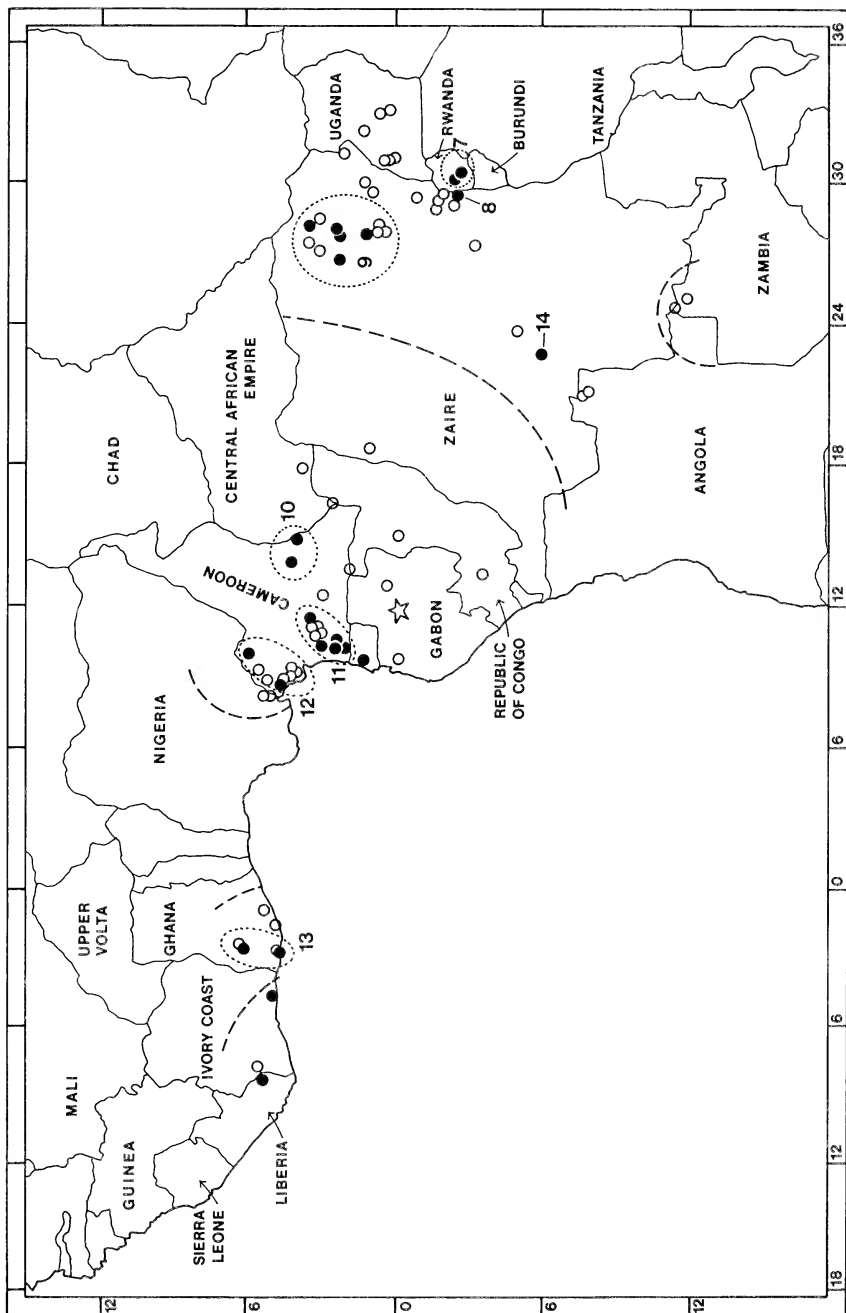
Taxonomic Conclusions

Based on our analyses of geographic variation and a study of specimens from sympatric situations, we consider the genus *Malacomys* to consist of two morphologically distinct species. In addition, based on the description, we accept *M. verschureni* as yet a third species. Of the specimens analyzed, the smaller western populations belong to the species *Malacomys edwardsi* De Rochebrune, and the larger eastern populations to *M. longipes* A. Milne-Edwards. *Malacomys verschureni* Verheyen and Van Der Straeten is known only from the type locality in eastern Zaire. Although *Malacomys edwardsi* exhibits little geographic variation, being small for the genus and rather uniform in size, and must be considered a monotypic species, *M. longipes* is characterized by a high degree of geographical variability. Three subspecies are recognizable by us at this time and two more nominal subspecies are included pending further study.

In the east, from northeastern Angola, Rwanda, Uganda, and extreme eastern, northeastern and southcentral Zaire, can be found *Malacomys longipes centralis*, with *M. l. wilsoni* as a synonym. This subspecies is characterized by large size in both external and cranial characters. The nominate subspecies, *M. l. longipes*, occurs in south-

←

Fig. 2.—Distribution of two species of *Malacomys*: triangles = *M. edwardsi*, circles = *M. verschureni*. Closed symbols represent localities of specimens examined, open symbols those of literature records. Because of undue crowding, not all records are plotted. Geographical samples (OTUs) are indicated by localities enclosed in dotted lines and numbered respectively. See the text for list of localities included in each OTU.



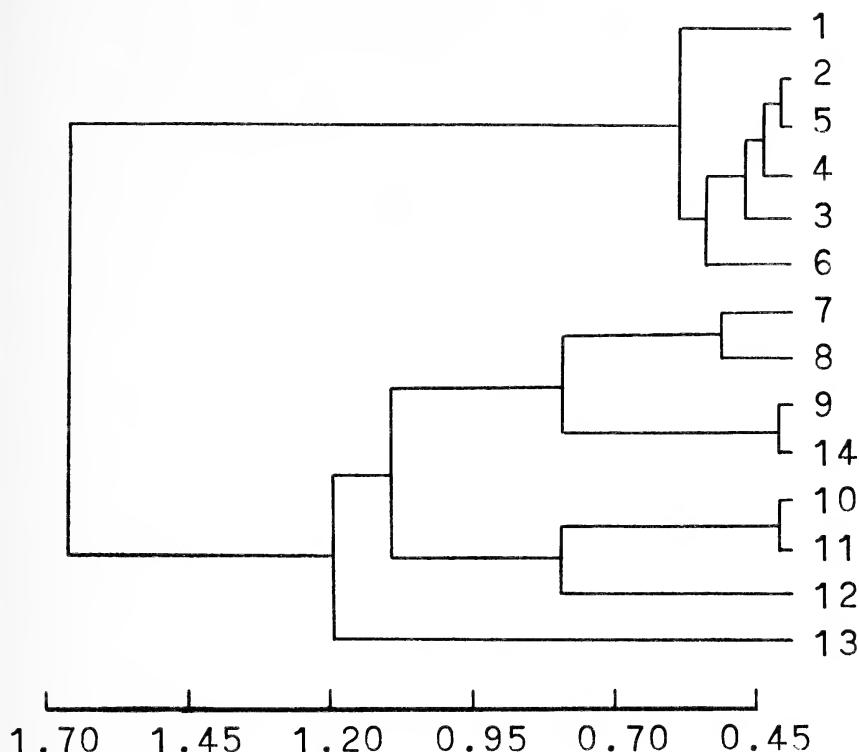


Fig. 4.—Distance phenogram resulting from cluster analysis of 14 geographical samples (OTUs) of *Malacomys*. See Figs. 2 and 3 and text for key to geographic samples. The cophenetic correlation for the phenogram equals 0.846.

eastern Nigeria, Cameroon, Central African Empire, western Zaire, Republic of Congo, Gabon, and Rio Muni; it is characterized by medium size in both external and cranial measurements. The third subspecies, *M. l. cansdalei*, known from southern Ghana, is much smaller in most dimensions than either *M. l. longipes* or *M. l. centralis*. Two additional subspecies are given tentative recognition. *Malacomys longipes australis* is known from Zambia, whereas *M. l. giganteus* is retained for specimens from southern Ivory Coast and eastern Liberia.

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Fig. 3.—Distribution map of *Malacomys longipes*. The type locality is indicated by an open star. See legend of Fig. 2 for details of symbols and numbers, and text for list of localities included in each OTU.

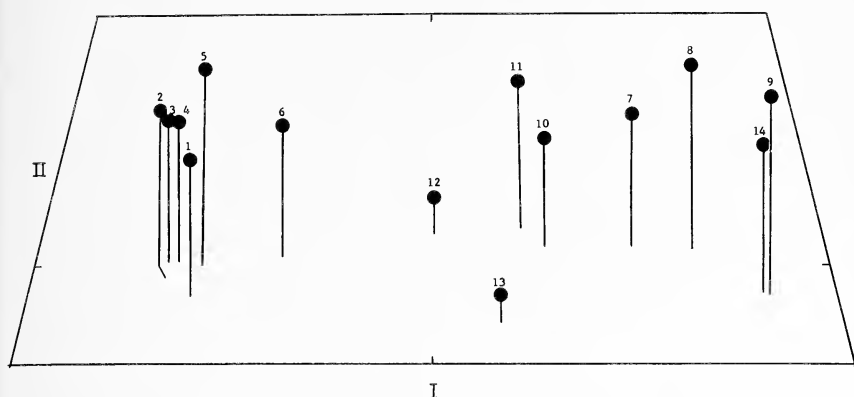


Fig. 6.—Three-dimensional projection of the first three principal components, showing the phenetic position of 14 geographical samples (OTUs) of *Malacomys*. See Figs. 2 and 3 and text for key to geographic samples. Component III is represented by length of line below dots. Component I accounts for 76.03% of the total variation, component II for 10.72% and component III for 4.04% for a combined total of 90.79% of the total variation.

SYNOPSIS OF SPECIES

In addition to a brief diagnosis and account of the genus *Malacomys*, the three recognized species in the genus are briefly discussed in the following accounts; the account of *M. longipes* is divided by subspecies. Relevant commentary is given on distribution and taxonomic remarks; lists of specimens examined and literature records finish the accounts.

Genus *Malacomys* A. Milne-Edwards

Malacomys A. Milne-Edwards, Bull. Soc. Philomath., Paris, (6)13:9, 1877.

Type species.—*Malacomys longipes* A. Milne-Edwards, 1877.

Diagnosis.—Characterized cranially by long narrow skull with elongated rostrum, dorsally flat in profile; braincase relatively narrow, not much wider than rostrum; anterior palatine foramina short, not extending anteriorly near the incisors nor posteriorly to level of first molar, and with foramina relatively broad; toothrows strongly reduced relative to length of skull; incisors smooth on anterior edge; zygomatic arch with small flanged edge; zygomatic plate not noticeably narrowed and only slightly cut back dorsally; supraorbital ridges barely traceable; and bullae small relative to size of skull. Externally, limbs are long and slender, particularly hindlimbs, with metatarsals elongated and loosely connected; ears large, rounded distally, naked and translucent; tail long and essentially naked; body slender to slightly robust, covered with soft pelage of medium length, on the midback about 10 mm in length and on the mid-belly about five mm; guard hairs absent in pelage; underfur and bristle fur not differentiated.

Distribution.—An inhabitant of the tropical high-forest block of Africa from Sierra Leone and Guinea eastwards as far as riparian forests of Uganda; thence southwards

Table 4.—Factor matrix showing character loadings on the first three principal components among 19 quantitative characters studied. Those characters showing a strong influence on a particular component are marked by an asterisk while those showing a lesser degree of influence are marked by an asterisk within parentheses. Abbreviations for characters are defined in materials and methods section in text.

Measurements	Factor component I	Factor component II	Factor component III
TL	0.817(*)	0.374	0.096
TA	0.700(*)	0.565(*)	-0.273(*)
HF	0.762(*)	0.448(*)	-0.179
EA	0.014	0.876*	0.159
GLS	0.962*	0.011	0.151
CBL	0.963*	0.055	0.184
GZB	0.973*	-0.131	0.010
LIB	0.944*	-0.290	0.051
BBC	0.793(*)	0.238	-0.441*
GLN	0.886(*)	-0.062	0.240
HOR	0.951*	0.071	0.000
LAP	-0.666	0.566(*)	0.397(*)
CLT	0.920*	0.127	-0.014
BOP	0.954*	0.148	0.010
LOP	0.949*	-0.116	0.171
GHS	0.944*	-0.047	-0.171
MTR	0.959*	-0.186	-0.088
HOM	0.927*	-0.139	0.288(*)
LOM	0.961*	-0.106	0.091

as far as riparian forests of northeastern Angola and northwestern Zambia (Figs. 2 and 3).

Malacomys edwardsi De Rochebrune, 1885

1885. *Malacomys edwardsi* De Rochebrune, Bull. Soc. Philomath., Paris, (7)9:87.

Type locality.—"Mellacoree" [=Melikhouré River, Guinea].

Distribution.—Sierra Leone, Guinea, Liberia and southern parts of Ivory Coast, Ghana, and Nigeria (Fig. 2).

Remarks.—*Malacomys edwardsi* can be distinguished from *M. longipes* by having smaller dimensions, both externally and cranially (Tables 2 and 3, Figs. 1, 4, 6, and 7). Particularly useful for differentiation from *M. longipes* are the small hindfoot, short length of skull, narrow interorbital breadth, relatively long anterior palatine foramina, and short length of maxillary and mandibular toothrows. For comparisons with *M. verschureni*, see the account of that species.

The only karyological information reported for the genus *Malacomys* is for *M. edwardsi* from an unknown locality in Ivory Coast. Matthey (1958) published a karyotype consisting of a diploid number of 48. All the chromosomes, including the sex chromosomes, were acrocentric.

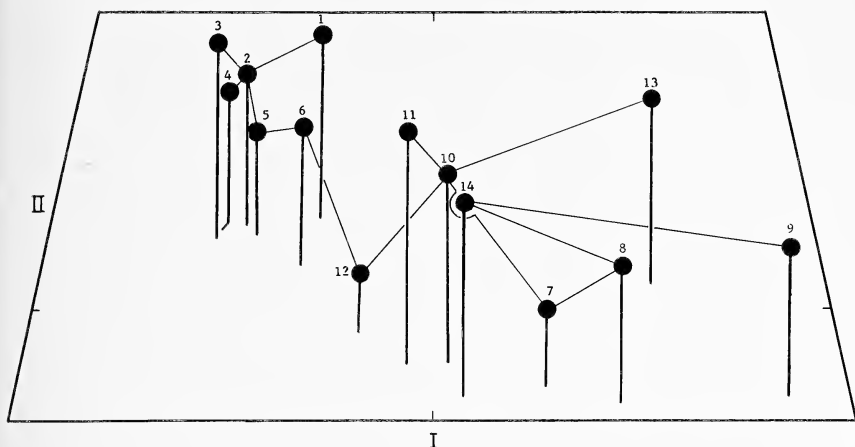


Fig. 7.—Three-dimensional projection of first three components of minimum distance scale, showing the phenetic position of 14 geographical samples (OTUs) of *Malacomys*. See Figs. 2 and 3 and text for key to geographic samples. Component III is represented by length of line below dots. The minimum spanning tree is superimposed onto the plot as lines connecting the dots. The stress value for the projection is 0.021.

Specimens examined (81).—**LIBERIA**: Tars Town, 25 km N Zwedru, 1 (USNM). **IVORY COAST**: Adiopodoume, 3 (AMNH); Blekoum, 9 (USNM); Duekove, 1 (AMNH); Ehania, 1 (USNM); Niebe, 5 (USNM); Soubre, 9 (USNM); Yabrasso, 1 (USNM); Yapo Sud, 4 (USNM). **GHANA**: Abamso, 1 (USNM); Berekuso, 11 (USNM); Efumumkrom, 3 (USNM); Gubinja, 1 (USNM); Kade, 2 (USNM); 5 mi N Kade, 6 (USNM); Nkawkaw, 5 (USNM); Oda, 6 (USNM); 32 mi W Prestea, 4 (USNM); Prince's Town, 2 (USNM). **NIGERIA**: 30 mi W Benim, 1 (USNM); Nikrowa, 1 (USNM); Sapoba, 4 (USNM).

Additional records.—**SIERRA LEONE**: Mount Bintamane (Rosevear, 1969:320). **GUINEA**: Melikhoure River (De Rochebrune, 1885:87); Mount Nimba (Heim de Balsac and Lamotte, 1958:350, 352; Rosevear, 1969:320). **LIBERIA**: Mount Barclay, Begwai, Gonyon, Deaple, Freemantown, Mount Grand Cape, Kahnple (Kuhn, 1965:331); Mount Coffee (Miller, 1900:644; Kuhn 1965:331); Bassa (Allen and Coolidge, 1930:602); Begwai, Mount Barclay, Gonyon (Rosevear, 1969:320). **IVORY COAST**: Adiopodoume (Heim de Balsac and Aellen, 1965:736); Lamto (Bellier, et al., 1972:310); Tai Forest (Dosso, 1975:516); no specific locality (Matthey, 1958). **GHANA**: Ankasa River Forest Reserve, Bobiri (Rosevear, 1969:320); Mampong (Hayman, 1936:932; Rosevear, 1969:320); Ankasa River Forest Reserve, Pra Suhien Forest Reserve, Sefwi Wiawso, Oda (Cole, 1972:617); Fure River Forest Reserve (Cole, 1975:458); Pampramase, Bia Tributaries North Forest Reserve, Area 14 (Jeffrey 1975:960). **NIGERIA**: Idanre, Lagos, Nikrowa Forest Reserve (Rosevear, 1969:320).

***Malacomys longipes australis* Ansell, 1958**

1958. *Malacomys longipes australis* Ansell, Ann. Mag. Nat. Hist., (13)1:340.

Type locality.—Sakeji stream, Mwinilungo district, Zambia.

Distribution.—Known only from the vicinity of the type locality in the northwestern tip of the Mwinilungo district of Zambia (Fig. 3).

Remarks.—Ansell (1958:340) described *M. l. australis* based on a number of characteristics, most of which refer to coloration of the pelage and were considered by him to represent one limit of clinal variation. As described, this subspecies is uniformly dull brown, lacking the reddish tone of other subspecies. Initially, Ansell (1958:340) considered facial markings to be constant and important but, after examining more specimens from the type locality, Ansell (1965:40) found these markings to be variable in size and degree of presence. The tail is strongly bicolored, with the white ventral color sometimes continuing onto the distal dorsal portion giving this portion of the tail a mottled effect. The color of the ventral pelage is more slate-colored than is found in other subspecies. Although the interorbital width was described as similar, the braincase was broader than in *M. l. wilsoni*. However, Ansell (1958:342) admitted that there was considerable individual variation in the skulls of the series of four adults and two juveniles. A table of measurements published later by Ansell (1965:41) indicates that this subspecies is large and has a long maxillary tooththrow for the species (6.1, 6.2, 6.3 for three adults).

We hesitate to comment on the validity of these pelage characteristics for this subspecies at this time. However, our examination of the pelage of other subspecies indicates that color does vary individually but not in a way where pelage color can be considered diagnostic when series are examined.

Specimens examined.—None.

Additional records.—ZAMBIA: Sakeji stream, Isombo stream (Ansell, 1958:340); Sakeji stream (Ansell, 1965:40).

***Malacomys longipes cansdalei* Ansell, 1958**

1958. *Malacomys longipes cansdalei* Ansell, Ann. Mag. Nat. Hist., (13)1:42.

Type locality.—Oda, Ghana.

Distribution.—Known from southern Ghana (Fig. 3).

Remarks.—*Malacomys longipes cansdalei* was originally proposed by Ansell (1958:342) based upon the greater degree of white found in the ventral pelage. Mensurally, the clinal decrease in size of *M. longipes* from east to west ends with *M. l. cansdalei* (Tables 2 and 3, and Figs. 1, 4, 6, and 7). Detailed comparisons with *M. longipes giganteus* of Ivory Coast and Liberia were not possible at this time. Nevertheless, Cole (1972) reported that *M. l. giganteus* was larger externally than *M. l. cansdalei*. Our results of geographic variation show that *M. l. cansdalei* has a hindfoot averaging larger than any of the more eastern samples of *Malacomys* analyzed. In addition, the same results indicate that, for breadth of braincase and length of anterior palatine foramina, *M. l. cansdalei* (OTU 13) averages larger than any other *M.*

longipes sampled. For other measurements, this subspecies was shown to be the smallest of the subspecies of *M. longipes* examined.

We have concluded that *M. l. cansdalei* differs only subspecifically from the more easterly *Malacomys longipes*. *M. l. cansdalei* is sympatric with *M. edwardsi*. However, *M. l. cansdalei* is separated from the nearest Nigerian localities of *M. longipes longipes* by nearly 900 km. This hiatus in distribution led Rosevear (1969) to question whether *M. l. cansdalei* might be a distinct species. Our results do not justify this potential separation. The results depicted on Fig. 4 can be interpreted in a number of ways but we prefer to separate the lower grouping into three subspecies at about the 0.95 level of phenetic distance. The OTUs depicted on Fig. 6 can be grouped into basically four groups with OTU 13 as the single representative of one of three groups on the right half of the figure.

Specimens examined (11).—GHANA: Ghiriso, 1 (USNM); Ankasa River Forest Reserve, 10 (USNM).

Additional records.—GHANA: Oda (Ansell, 1958:342; Rosevear, 1969:319); Ankasa River Forest Reserve (Rosevear, 1969:319; Cole 1972:617); Pra Suhien Forest Reserve, Sefwi Wiawso (Cole, 1972:617); Fure River Forest Reserve (Cole, 1975:454).

***Malacomys longipes centralis* De Winton, 1897**

1897. *Malacomys centralis* De Winton, Ann. Mag. Nat. Hist., (6)19:465.

1916. *Malacomys wilsoni* Thomas, Ann. Mag. Nat. Hist., (8)18:238. Type locality: In-kogon-kakese, Zaire. *New Synonymy*.

Type locality.—Tingassi, Mombuttu [district], Zaire.

Distribution.—Occurring in northeastern Angola, Rwanda, Uganda, and extreme eastern, northeastern, and southcentral Zaire (Fig. 3).

Remarks.—Judging from the results of our analysis of geographic variation (Figs. 1, 4, 6, and 7, and Tables 2 and 3), we are unable to separate *Malacomys wilsoni* Thomas (represented by OTU 14 on Fig. 3) from *Malacomys centralis* De Winton (represented by OTU 9 on Fig. 3). *Malacomys wilsoni* is placed in synonymy under *M. centralis*. All the *Malacomys longipes* from eastern, northeastern, and southcentral Zaire, Uganda, Rwanda, and northeastern Angola are considered to be *M. l. centralis* based on this analysis of geographic variation. This subspecies is characterized by large size, both externally and cranially, for the species. Measurements of this subspecies tend to be the maximum for the species, reaching the highest limit of variation. Based on the measurements of *M. l. australis* published by Ansell (1958:343, 1964:41), it appears that this subspecies also is large for the species and close to *M. l. centralis* in size.

Specimens examined (87).—RWANDA: 110 km W Butare, 1; Uinka, 6 (USNM). ZAIRE: Avakubi, 3 (AMNH); Gamangui, 29 (AMNH); Lemera, 13 (USNM); Luluabourg, 24 (AMNH); Medje, 3 (AMNH); Niangara, 4 (AMNH); Niapu, 4 (AMNH).

Additional records.—ANGOLA: Parque Carisso, near Dondo (Sanborn, 1952:114; Hayman, 1963:126); Reviere Nefu, 50 km S Dondo (Sanborn, 1952:114). RWANDA: Regege (Rahm, 1966:108); Nakalonge, Uinka (Rahm, 1967:471). UGANDA: Mpanga Forest, Fort Portal (Thomas and Wroughton, 1910:511; Misonne, 1963:41); Mpanga Forest, Zika Forest (Southern and Hook, 1963:127); Kabanyolo, Kalinzu Forest, Mpanga Forest, Zika Forest (Delany and Neal, 1969:327); Kalinzu Forest, Mpanga Forest, Kabanyolo, Mayanja Forest, Zika Forest (Delany, 1975:90). ZAIRE: Avakubi, Bambara, Bwana-sura, Gamangui, Listmu, Niangara (Hatt, 1940:503); Lemera, Bushushu, Kahuzi Mountain, Tshamola, (Rahm and Christiaensen, 1963:75); Lemera, Tshabondo, Kahuzi, (Rahm, 1967:471); Hambo, Irangi, Kisanga, Mulundu, Niamiringi (Rahm, 1966:108); Inkongokakase (Thomas, 1916:238); Ituri Forest (Ansell, 1958:342); Tingase (Thomas, 1888:11; De Winton, 1897:466; Hatt, 1940:503); Medje, Poko (Thomas, 1915:476; Hatt, 1940:503); Luluabourg (Cabrera and Ruxton, 1926:599); Kartoushi (Gyldenstolpe, 1928:74; Misonne, 1963:41); Bambara (Schwarz, 1920:1070); Fundi, Mambaka, Pili Pili (Dollman, 1914:85; Hatt, 1940:503); Luebo (Kershaw, 1923:367).

Malacomys longipes giganteus Bellier
and Gautun, 1968

1968. *Malacomys longipes giganteus* Bellier and Gautun, Mammalia, 32:80.

Type locality.—Banco Forest, Ivory Coast.

Distribution.—Known from eastern Liberia and southern Ivory Coast (Fig. 3).

Remarks.—We are following Cole (1972) in retaining this subspecies, as no direct comparisons between adults was possible. Both specimens from Ivory Coast had no skulls available when examined. The single Liberian specimen was a subadult but was, nevertheless, clearly an example of *M. longipes* based upon its large size. This Liberian specimen, trapped by the junior author on 4 July 1971 near a small stream in secondary forest, represents the westernmost record of this species in West Africa. An adult *M. edwardsi* was taken in the same place near the stream on 8 July 1971.

Specimens examined (3).—LIBERIA: Tars Town, 25 km N Zwedru, 1 (USNM). IVORY COAST: Banco Forest, 2 (USNM).

Additional records.—IVORY COAST: Banco Forest (Bellier and Gautun, 1968:80); Tai Forest (Dosso, 1975:516).

Malacomys longipes longipes
A. Milne-Edwards, 1877

1877. *Malacomys longipes* A. Milne-Edwards, Bull. Soc. Philomath., Paris, (6)13:9.

Type locality.—Gaboon [Gabon] River, Gabon (restricted more specifically to vicinity of Ogooue, Gabon, by De Pousargues, 1897:7, 9).

Distribution.—Occurring in southeastern Nigeria, Cameroon, Central African Empire, Republic of Congo, western Zaire, Gabon, and Equatorial Guinea (Rio Muni) (Fig. 3).

Remarks.—The nominate subspecies is characterized by medium size for the species for most measurements. The exception to this trend

in geographic variation is found in the length of hindfoot where *Malacomys longipes longipes* is small for the species (Figs. 1, 4, 6, and 7, and Tables 2 and 3).

We are unable to explain the nearly 900 kilometer hiatus in distribution between *M. l. longipes* of southeastern Nigeria and *M. l. cansdalei* of southern Ghana. This hiatus might be attributed to the effect of the Dahomey Gap but if this were true, this distribution would indicate the Gap is of fairly recent origin as the geographic distribution of both *M. longipes* and *M. edwardsi* are interrupted in this area. Yet this entire intermediate region has been collected extensively in recent years by collectors from the Smithsonian Institution, Washington, D.C., and the Rijksuniversitair Centrum, Antwerp, Belgium, and no specimens of *Malacomys* have been reported.

Specimens examined (40).—CAMEROON: Batanga, 10; 30 km W Bertoua, 1 (AMNH); Bipindi, 3 (AMNH); Ebolowa, 4; Efulan, 3 (1 AMNH); 8 km SW Eseka, 2; Kribi, 2; Lolodorf, 9; 12 km SE Mamfe, 1 (AMNH); Nyabessan, 1; 2 km S Saa, 1 (AMNH); Yaounde, 1. EQUATORIAL GUINEA (RIO MUNI): 14 mi from mouth Benito River, 2 (USNM).

Additional records.—NIGERIA: Basho, Okoiyong (Sanderson, 1940:712). CAMEROON: Benito, Kribi, Bitye (Schwarz, 1920:1065); Akak, Campo (Monard, 1951:27); Batoki, Malende, Isobi, N'dian (Rosevear, 1969:319); Bitye, Efulen, Mamfe (Rosevear, 1969:320); Ekundu (Sjostedt, 1897a:29; Sjostedt, 1897b:14); Eshobi, Tinta (Sanderson, 1940:712); Foullassi, 6 km NNW Sangmelima (Perret and Aellen, 1956:424). CENTRAL AFRICAN EMPIRE: Lidjombo (De Beaufort, 1962:199); La Maboque (Compoint-Monnignaut, 1968:524; Petter and Genest, 1970:452). REPUBLIC OF CONGO: Etoumbi (Malbrant and MacLachy, 1949:277); Mibla (Petter, 1967:819). GABON: Gabon River (A. Milne-Edwards, 1877:9); Ogooue (De Poussargues, 1897:7); Makokou (Dubost, 1968:231); Como River (Rosevear, 1969:321). EQUATORIAL GUINEA (RIO MUNI): no specific locality (Cabrera, 1908:453). ZAIRE: Mabondo (Rahm, 1966:108).

***Malacomys verschureni* Verheyen and Van Der Straeten, 1977**

1977. *Malacomys verschureni* Verheyen and Van Der Straeten, Rev. Zool. Afr., 91(3):739.

Type locality.—Mamiki, Republic of Zaire (approx. 0°40'N, 29°35'E).

Distribution.—Known only from the holotype (Fig. 2).

Remarks.—Verheyen and Van Der Straeten (1977:741) distinguished this new species from *Malacomys longipes* and *M. edwardsi* by its flat profile of the nasal region, the pointed posterior ends of the palatine foramina, and very strongly developed exterior processes of the mandible, but cautioned that variability of these characters could not be accurately assessed with only one specimen. Further, *M. verschureni* can be distinguished by its small external measurements, the occurrence of six (rather than five) plantar tubercles, and the presence of a very small T₃ on M² and a T₉ on M¹ and M². Verheyen and Van Der

Straeten (1977:741) found these cusps to occur very seldom in other *Malacomys*.

Mensurally, *M. verschureni* is small for the genus, approaching *M. edwardsi* in size. But it is widely separated geographically from *M. edwardsi*, whose geographic range reaches eastward only to south-central Nigeria (Fig. 2). The following selected external and cranial measurements (in millimeters) are from the description by Verheyen and Van Der Straeten (1977:742): head and body length, *ca.* 120; length of tail, 132; length of hindfoot, 29 (*c.u.*); length of ear, 20; greatest length of skull, 33.95; zygomatic breadth, 15.45; least interorbital breadth, 5.05; breadth of braincase, 12.70; greatest length of nasals, 14.00; length of anterior palatine foramina, 6.20; length of upper cheekteeth, 5.45; breadth of upper dental arch, 5.90; and length of lower cheekteeth, 5.00. When the above measurements are compared to those in Table 2, the following—total length, length of tail, length of hindfoot, length of ear, greatest length of skull, least interorbital breadth, breadth of braincase, and length of nasals—fall below or just within the minimum range of those same measurements for *M. edwardsi*. From the published measurements, *M. verschureni* seems to have a short skull and relatively long rostral region but with a wide zygoma and a narrow interorbital region. The upper and lower cheekteeth are relatively long, falling within the range of measurements of the cheekteeth for *M. longipes*.

Specimens examined.—None.

Additional records.—ZAIRE: Mamiki, NNE of Beni (Verheyen and Van Der Straeten, 1977:739).

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GAZETTEER

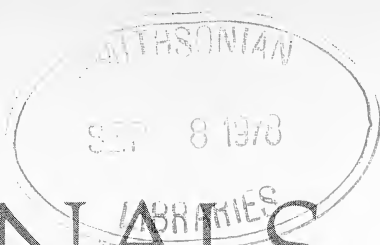
The localities from which specimens were examined and those cited from the literature are listed alphabetically below. The spelling of place names consistently follows that given in the gazetteers published by the United States Board on Geographical Names. In most instances, coordinates listed are those given in the above mentioned gazetteers. However, when more than one occurrence of a place name existed, Davis and Misonne (1964) was consulted for more specific information. In a few instances authors published coordinates for localities; however, if these coordinates varied considerably from those given in the Board on Geographical Names' gazetteers, the latter was followed. All of the localities listed were plotted although not always precisely, on the distribution maps (Figs. 2 and 3 in text). Localities for which no coordinates could be found have been left blank. Abbreviations used in the gazetteer are: Mt = Mountain or Mount; A = Angola; B = Benin; CAE = Central African Empire; CM = Cameroon; CR = Republic of Congo; EG = Equatorial Guinea (Rio Muni); GA = Gabon; GH = Ghana; GU = Guinea; IC = Ivory Coast; L = Liberia; N = Nigeria; R = Rwanda; SL = Sierra Leone; U = Uganda; ZM = Zambia; ZR = Zaire.

Abamso, GH	05 05N; 01 45W
Adiopodoume, IC	05 20N; 04 07W
Akak, CM	02 23N; 10 00E
Ankasa River Forest Reserve, GH	05 17N; 02 35W
Avakubi, ZR	01 19N; 27 33E
Bambara, ZR	03 51N; 27 00E
Banco, Parc National du, IC	05 25N; 04 03W
Barclay, Mt., L	06 22N; 10 40W
Basho, N	06 08N; 08 25E
Bassa, L	05 52N; 10 05W
Batanga, CM	04 10N; 14 28E
Batoke, CM	04 03N; 09 06E
Begway, L	05 53N; 10 05W
Benim, N	06 20N; 05 38E

Benito, CM	
Benito River, 15 mi. from mouth, EG	01 35N; 10 30E
Berekuso, GH	05 45N; 00 13W
Bertuoa, CM	04 35N; 13 41E
Bintamane Mt. (=Loma Mansa Mt), SL	09 13N; 11 07W
Bipindi, CM	03 05N; 10 25E
Bitye, CM	03 01N; 12 22E
Blekoum, IC	06 29N; 03 39W
Bobiri, GH	
Bushushu, ZR	03 01S; 28 54E
Butare, R	02 36S; 29 44E
Bawana-sura, ZR	01 04N; 29 35E
Campo, CM	02 20N; 09 50E
Coffee, Mt., L	06 30N; 10 35W
Como River, CR	00 15N; 10 11E
Deaple, L	
Duekove, IC	06 45N; 07 21W
Ebolowa, CM	02 54N; 11 09E
Efoulán, CM	02 47N; 10 32E
Efumumkrom, GH	05 43N; 01 49W
Ehania, IC	05 14N; 02 46W
Ekundu, CM	04 41N; 08 57E
Eseka, CM	03 35N; 10 44E
Eshobi, CM	05 47N; 09 23E
Etoumbi, CR	00 01N; 14 49E
Fort Portal, U	00 40N; 30 17E
Foulassi, CM	02 57N; 11 57E
Freemantown, L	
Fundi, ZR	02 06N; 20 46E
Fure River Forest Reserve, GH	05 25N; 02 20W
Gabon River, GA	00 10N; 09 45E
Gamangui, ZR	02 10N; 27 15E
Ghiriso, GH	06 32N; 02 20W
Gonyon, L	05 53N; 10 05W
Grand Cape, Mt., L	06 41N; 11 20W
Gubinja, GH	07 45N; 02 04W
Hombo, ZR	01 52S; 28 27E
Idanre, N	06 43N; 05 06E
Inkongo-kakese, ZR	04 53S; 23 18E
Irnagi, ZR	01 54S; 28 27E
Isombo Stream, ZM	ca. 11 00S; 24 00E
Isobi, CM	04 11N; 09 00E
Ituri Forest, ZR	01 00N; 29 16E
Kabanyolo, West Mengo, U	00 30N; 32 15E
Kade, GH	06 05N; 00 50W
Kahnple, L	07 17N; 08 30W
Kahuzi Mt., ZR	02 15S; 28 40E
Kalinzu Forest, U	00 25S; 30 05E
Kartoushi, ZR	
Kisanga, ZR	03 05S; 26 58W

Kribi, CM	02 45S; 10 15E
Kunungu, ZR	02 06S; 16 26E
Lagos, N	06 27N; 03 23E
La Mabohe, CAE	03 45N; 17 53E
Lamto, IC	06 12N; 04 58W
Lemera, ZR	02 08S; 28 50E
Lidjombo, CAE	02 41N; 16 06E
Listmu, ZR	
Lolodorf, CM	03 14N; 10 44E
Luebo, ZR	05 30S; 29 45E
Luluabourg, ZR	05 45S; 22 25E
Mabondo, ZR	01 14N; 18 18E
Makokou, GA	00 40N; 12 50E
Malende, CM	04 20N; 09 26E
Mambaka, ZR	00 51N; 27 33E
Mamfe, CM	05 46N; 09 17E
Mamiki, ZR	00 40N; 20 35E
Mampong, GH	07 04N; 01 24W
Mayanja Forest, U	01 21N; 31 49E
Mbila, CR	03 12S; 13 20E
Medje, ZR	02 25N; 27 18E
Melikhoure River, GU	09 10N; 13 10W
Mpanga Forest, U	00 03N; 30 17E
Mulundu, ZR	00 56S; 28 28E
Nakalonge, R	
N'dian, CM	04 57N; 08 52E
Niamiringi, ZR	
Niagara, ZR	03 24N; 27 52E
Niapu, ZR	02 25N; 26 28E
Niebe, IC	05 22N; 07 18W
Nikrowa, N	06 14N; 05 21E
Nimba, Monts, GU	07 38N; 08 28W
Nkawkaw, GH	06 33N; 00 46W
Nyabessan, CM	02 24N; 10 24E
Oda, GH	05 55N; 00 59W
Ogooue, GA	00 03S; 11 58E
Okoiyong, N	05 45N; 08 25E
Pampramase, GH	ca. 06 38N; 02 57W
Parque Carisso, A	07 49S; 20 57E
Pili Pili, ZR	00 33N; 27 44E
Poko, ZR	03 08N; 26 54E
Pra Suhien Forest Reserve, GH	05 21N; 01 23W
Prestea, GH	05 26N; 02 09W
Prince's Town, GH	04 47N; 02 08W
Reviere Nefu, A	07 45S; 20 45E
Rugege, R	02 15S; 29 14E
Saa, CM	06 36N; 11 05E
Sakeji Stream, ZM	11 07S; 24 20E
Sapoba, N	06 06N; 05 53E
Sefwi Wiawso, GH	06 17N; 02 28W
Soubre, IC	05 47N; 06 36W

Tafou, Pointe, IC	04 24N; 07 21W
Tai Forest, IC	05 45N; 07 12W
Tars Town, L	06 13N; 08 08W
Tshabondo, ZR	
Tingasi, ZR	03 10N; 28 00E
Tinta, CM	06 15N; 09 31E
Tshamola, ZR	02 01S; 28 53E
Unika, R (see Rugege)	
Yabrasso, IC	07 26N; 03 29W
Yapo Sud, IC	05 48N; 04 08W
Yaounde (Nkomekou), CM	03 52N; 11 31E
Younga, CAE	06 16N; 20 42E
Zika Forest, U	00 06N; 32 22E



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FLORAL VASCULAR ANATOMY OF *PLEEA TENUIFOLIA* MICHX. (LILIACEAE-TOFIELDIEAE) AND ITS REASSIGNMENT TO *TOFIELDIA*

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ABSTRACT

The floral vascular anatomy and floral morphology of *Pleea tenuifolia* Michx., a south-eastern coastal plain endemic, are reported, and compared to its Englerian tribal cohorts, *Tofieldia* and *Nartheceum*. In *Pleea*, an ensheathing bract and a three-parted, basally connate bracteole, both vascularized, are associated with each flower. Fusion bundles are not characteristic of the tepal, staminal, and gynoeceal vascularization. From a pedicel with an 18-bundled, cross-sectional, ring configuration, the floral parts are supplied by bundles of simple division. Basally each tepal receives three traces. Nine stamens with simple bundles are typical—six in the outer whorl, three in the inner whorl. The dorsals share a common basal bundle with the outer tepal median, whereas the ventral's common basal bundle is shared with the outer stamen bundles and the outer tepal laterals. The axial ventrals directly supply the ovules via horizontal funicular traces. Several gynoeceal features are significant. An intercarpellary gland formed within the upper pedicel opens externally and cuts off three, vascularized stipitate carpels. These three carpels are not fused laterally, only appressed via interdigitating papillae. In fruit, the carpels separate septically. The seeds are appendaged. Because of the extensive, reported similarities between *Pleea tenuifolia* and the genus *Tofieldia*, the former is transferred to the genus *Tofieldia*.

INTRODUCTION

The monotypic genus *Pleea* of L. C. Richard published by Michaux (1803) precedes *Pleea* of Persoon (1805). The only species in the genus, *P. tenuifolia* (rush featherling, star flower), has had a long taxonomic

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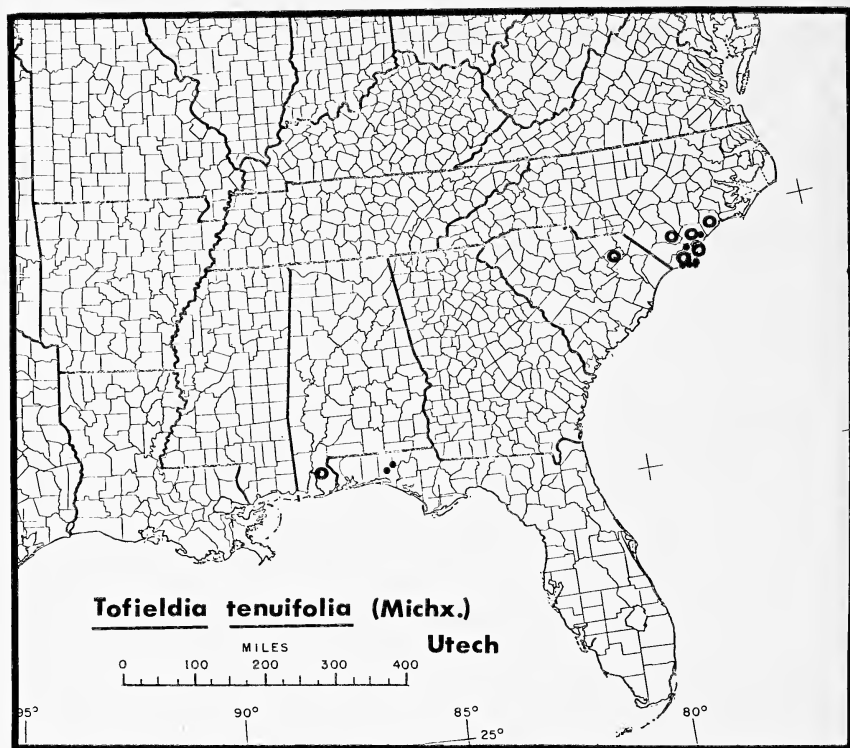


Fig. 1.—Distribution map of *Tofieldia tenuifolia* (Michx.) Utech based on examined and cited herbarium specimens (solid dots), and county records (open circles) mapped by Johnson (1969) and also based on herbarium specimens.

history as a coastal plain endemic (Wells, 1967; Small, 1933; Johnson, 1969; Radford et al., 1964). Though rare in the eastern United States, it is plentiful within its limited areas of occurrence on the southern, outer Coastal Plains (Fig. 1). It flowers in autumn, and occurs in pine-land swamps, grassy bogs, savannahs, and pocosins. The sites are usually open with acid soil. The shallow spreading rhizome system results in a close scattering of clones.

Beginning with Redouté's illustration (t. 25), which accompanied the type description (Michaux, 1803), several additional illustrations of *Plelea tenuifolia* have been presented (Redouté, 1808; Sims, 1818; Lamark, 1823; Small, 1933; Radford et al., 1964). Redouté's first illustration (t. 25) in Michaux (1803) is the same as that presented later in the massive *Liliacées* (Redouté, 1808; t. 456). The Lamark illustration (1823) is a modified version of the first Redouté illustration. Sims (1818)

used original material for his *Botanical Magazine* illustration (t. 1956). The floral line drawing in Small (1933) has inaccuracies.

Botanists in the past have expressed varying opinions on the relationship of *Pleea*. Richard (Michaux, 1803) noted a relationship to *Narthecium*, whereas Asa Gray (1836) indicated an affinity towards *Tofieldia* and *Zygadenus*. Both Engler (1888) and Krause (1930) have placed *Pleea* in a similarly circumscribed tribe, the Tofieldieae, which contains *Tofieldia* Hudson and *Narthecium* L. Hutchinson (1934, 1959), on the other hand, has used a larger tribe, the Narthecieae, to circumscribe *Pleea*, *Tofieldia*, *Narthecium*, and several other genera. The exact relationship of *Pleea* to *Tofieldia* and *Narthecium*, as well as the other genera of Hutchinson's Narthecieae, has not been adequately documented.

Gates (1918), while relating *Pleea* to *Tofieldia* (including the segregate genus *Triantha* (Nutt.) Baker) and *Narthecium*, makes a direct comparison with inferred relatedness to *Tofieldia* (*Triantha*). The major floral differences between *Pleea* and *Tofieldia* (*Triantha*) according to Gates (1918) are the lack of the three-parted connate pedicel bracteoles in *Pleea*, the outer subtending bract in *Pleea* is large and spathe-like, the stamen number in *Pleea* is higher, that is, nine to 12 in *Pleea* versus six for *Tofieldia* (*Triantha*), and the versatile anthers in *Pleea* are elongated.

This study is part of a continuing series of investigations on the primitive members of the Liliaceae (Utech and Kawano, 1978; Utech, 1978a, 1978b) and will present the floral vascular anatomy and morphology of *Pleea tenuifolia*. Particular detail will be given to the stamen number and morphology, which has historically isolated this species, as well as to the bracts and bracteoles of the raceme. A comparison to the other members of the Englerian Tofieldieae, that is, *Tofieldia* and *Narthecium*, will be made and evidence will be presented, which shows that *Pleea* should be considered a member of the genus *Tofieldia*.

MATERIALS AND METHODS

Collections of *Pleea tenuifolia* were made from two populations in North Carolina: Onslow Co., SW of Holly Ridge along US 17, pine savannah, (Utech 77-513 CM), and Pender Co., 4.0 mi NE of Hampstead on US 17, savannah, (Utech 77-515 CM). Flowering inflorescences were fixed in 3:1 (absolute ethanol: glacial acetic acid) for 10 h with subsequent storage in 70% ethanol. Standardized paraffin sections were cut between 14–16 μ and stained in safranin-methylene blue (Johansen, 1940; Sass, 1958). A total of 30 flowers of *P. tenuifolia* were sectioned, 15 from both populations. As an additional check on these serial sections, whole flowers were cleared and stained in a NaOH-1% fuchsin mixture (Fuchs, 1963).

The specimens used for the distribution map (Fig. 1) are cited at the end of the paper following Holmgren and Keuken (1974). Figs. 3–5 are composite photomicrographs which present the vascular floral anatomy of *P. tenuifolia*, whereas Figs. 6–9 are line-

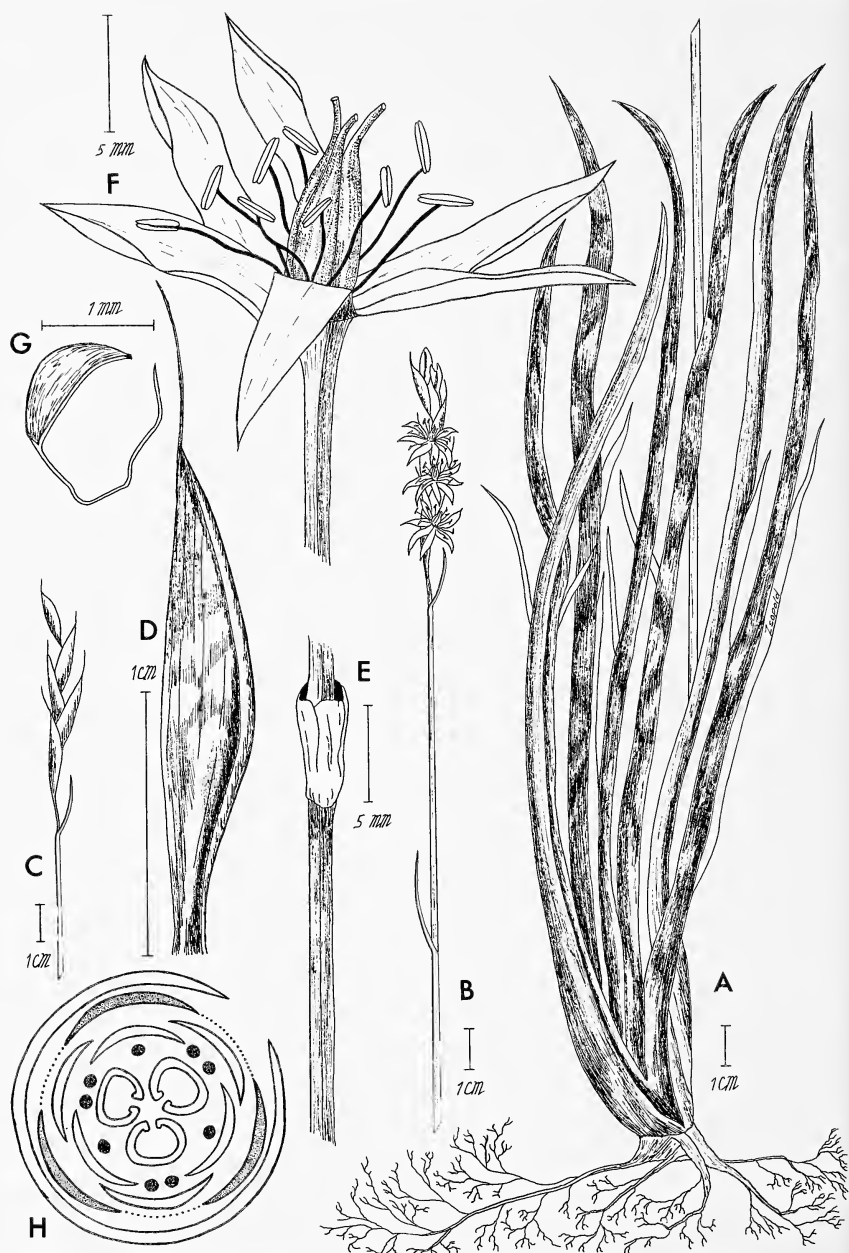


Fig. 2.—Illustration of *Tofieldia tenuifolia* (Michx.) Utech. A) Habit showing basal equitant leaves, fibrous root system, and simple scape. B) Flowering scape with three open flowers. C) Same scape as B with flowers and buds omitted to show the large, with a 1 cm scale bar.

drawn summary diagrams. No teleological implications are intended by the descriptive manner of vasculature presentation and discussion. The various bundles and traces are letter-coded for ease in comparison. This coding parallels that used in our previous liliaceous studies (Utech and Kawano, 1975, 1976a, 1976b, 1976c, 1978; Utech, 1978a, 1978b). For comparison Figs. 10–11 present past illustrated cross-sections of *Tofieldia* (Anderson, 1940; El-Hamidi, 1952). The cross-sections of *Nartheceum americanum* (Fig. 12) are from our unpublished data (Utech, unpublished manuscript). Following this vascular presentation, a tribal and generic taxonomic discussion will be presented, which concludes in the formal transfer of *Pleea tenuifolia* to the genus *Tofieldia*.

OBSERVATIONS

Inflorescence, Pedicels, Bracts, and Bracteoles

The fertile individuals of this rigid, subscapose perennial herb are usually (3.5)–5.5–7.0–(8.0) cm tall from a basal rosette of stiff, linear, equitant leaves. The larger leaves average 22.5 cm long (range: 15.0–30.0 cm) by 1.7 mm wide (range: 0.90–2.5 mm). The leaves are aristate tipped. Progressively smaller leaves occur upwards on the lower half of the scape.

The simple, terminal bractose raceme of *Pleea tenuifolia* usually has five to eight flowers, which are confined to the upper one-fourth of the total plant's height. The raceme has an interrupted appearance due to a series of large, green, erect, spathe-like bracts which ensheath the pedicels of each flower. The bracts have numerous parallel veins, decrease in size upwards and are marked with a prominent aristate tip (Fig. 2). The bract proper at a given node is consistently longer than its associated aristate tip. The average length of the lower three bracts is 2.3 cm (range: 1.1–2.8 cm), whereas the average length of its associated tip is 1.2 cm (range: 0.4–2.0 cm). Upwards there is a progressive decrease in bract length. A given bract is imbricated around the pedicel of the flower at that node, as well as the base of another bract that contains the pedicel of the flower for the node above. The total pedicel length of a given flower can only be observed by removing the ensheathing bract (Fig. 2).

The total pedicel length is slightly greater than that of the bract proper and slightly shorter than the total bract length. The average pedicel length for the three lowest flowers is 3.0 cm (range: 2.4–4.5 cm). When the bract is removed, a basally connate whorl of three bracteoles is observed near the middle to the upper one-third of the

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ensheathing bracts. D) Enlarged bract from mid-scape, prominent aristate tip. E) Pedicel and three-parted, basally connate bracteoles, both are normally hidden by the ensheathing bract. F) Enlarged flower showing the nine stamen configuration and the three free styles. G) Distally appendaged seed. H) Floral diagram that includes the bract and the bracteoles. (Scale indicated; drawing by Ms. Pamela J. Leopold)

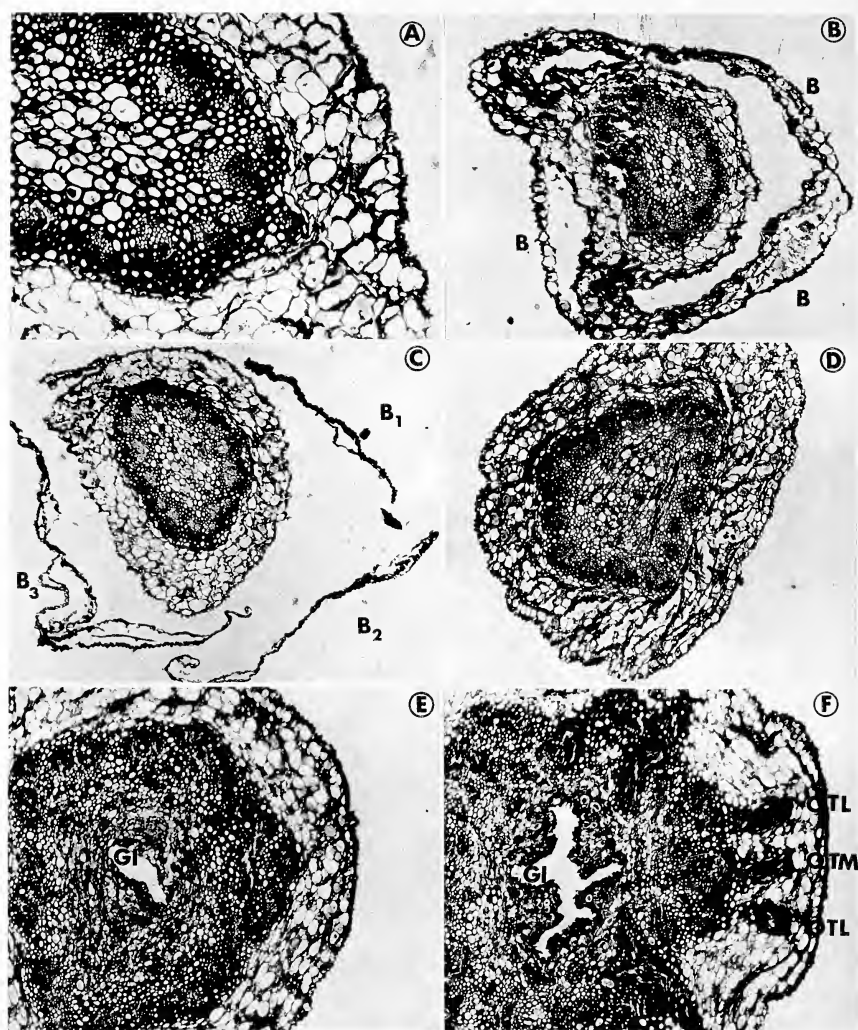


Fig. 3.—Cross-sectional series from *Tofieldia tenuifolia* (Michx.) Utech showing the vascularization of the pedicel and bracteole. A) Pedicel section below the level of bracteole formation; alternating bundles within the central ring establish outwardly the bracteole bundles and inwardly the pedicel supply; a sclerenchymatous sheath is associated with the vascular ring; the cells of the pith are differentiated from those of the cortex (40 \times). B) Slightly oblique section above A and showing both the basally connate bracteoles (B) and the partially freed pedicel (25 \times). C) Section above B; the central pedicel with its 18-bundled vascular ring is surrounded by the three, free, marginally imbricated bracteoles (B₁–B₃) (25 \times). D) Upper pedicel above the bracteoles; a sclerenchymatous sheath surrounds the vascular ring, as in A, and separates the undifferentiated cortex from the central pith (30 \times). E) Upper pedicel below the receptacle; the intercarpellary

pedicel (Fig. 2). These three-parted pedicel bracteoles are normally hidden by the ensheathing outer bract. The bracteoles are usually 1.0–1.5 cm long from their fused base to the ends of their freed tips (Fig. 2).

Below the three-parted bracteoles, the pedicel is circular in cross-section. At this level, the pedicel vascularization usually consists of a closely spaced ring of 18 bundles (Fig. 3A). Both the fruiting and flowering pedicels have a sclerenchymatous sheath around these bundles. The cells of the pith differ from those in the surrounding cortex, and it is within the former that the open, intercarpellary gland (GI) is formed (Figs. 3; 6 D–E; 7 D–E).

The pedicel vascularization above and below the insertion of the basally connate bracteoles is the same (Figs. 3 A–D; 6 A–C; 7 A–C). Below the level of bracteole attachment, a bundle is formed via division from each of the 18 pedicel bundles. These 18 derived bundles depart outward on alternating radii from the parental pedicel bundles. The connate bracteoles form a tube in lower cross-sections. At their mid-length they are subdivided into three free segments (Fig. 3 C). Basally each segment is associated with six of the 18 derived bundles (Figs. 6 A–D; 7 A–D). Not all of the six bundles per segment continue to the bracteole tips.

The joint occurrence of both bracts and bracteoles in *Pleea* is significant in a comparison between *Pleea* and *Tofieldia*. Vascular and morphological attention has been given to the bracteoles because they have frequently been omitted in past species descriptions. This “apparent” lack has been used in part for the taxonomic isolation of *Pleea*. Both Johnson (1969) and Radford et al. (1964) correctly reported the three connate bracteoles in *Pleea*, whereas Kunth (1843) noted two bracteoles, and Baker (1879) noted one to two bracteoles. Others reported none. Gates (1918), for example, stressed the “unobserved” absence of the bracteoles in *Pleea* as a difference between *Pleea* and *Tofieldia* (*Triantha*).

A survey of the species of *Tofieldia* shows a whole series of bract-bracteole combinations and reductions. Most species clearly have both, though in no case does a species of *Tofieldia* have a bract, which approaches the shape and size of that in *Pleea*. Frequently the shape and the size of the bracteoles in *Tofieldia* are similar to those in *Pleea*. The location of the bracteoles in *Tofieldia*, however, is normally directly below the flower, and appears as a second calyx (*calyculus*).

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gland (GI) opens centrally from within the pedicel's pith (35×). F) Lower, expanded receptacle showing the several arm branches of the intercarpellary gland (GI); peripherally the outer tepal vasculature departs, that is, the OTM and the OTL pair (40×).

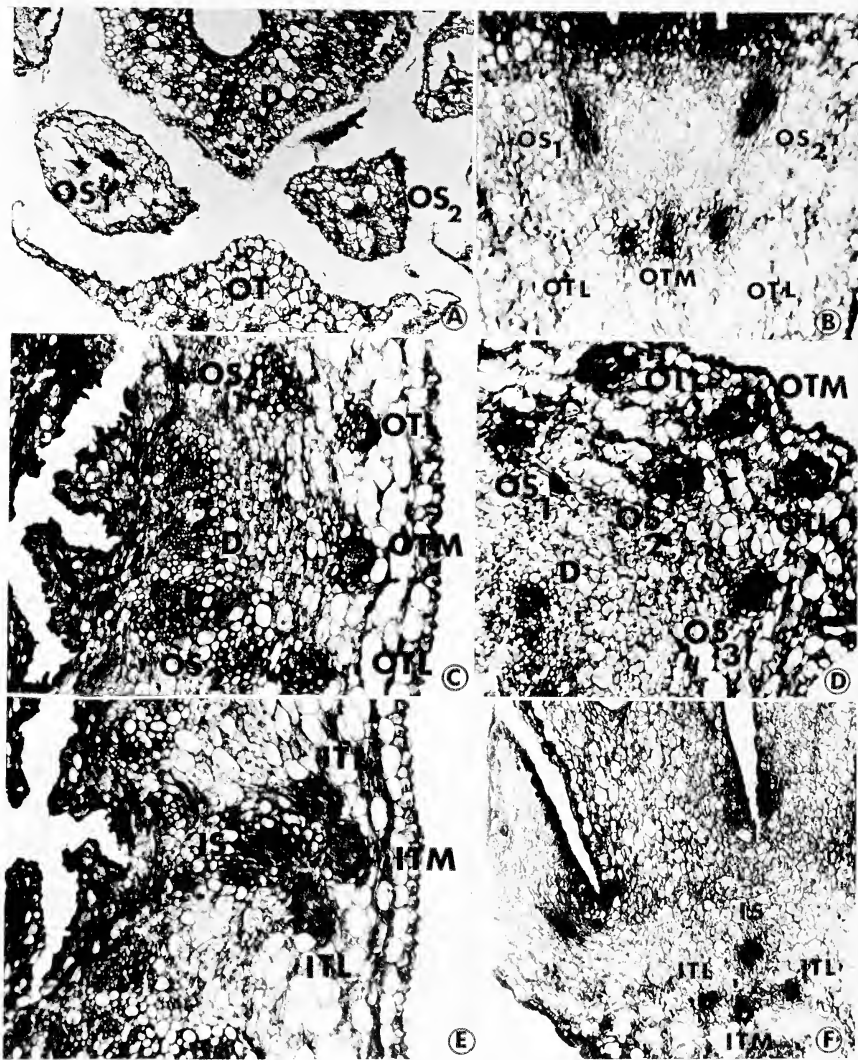


Fig. 4.—Outer and inner tepal and stamen vascularization in *Tofieldia tenuifolia* (Michx.) Utech. A) Cross-section at the level of freed tepals and stamens, as well as the carpellary stipes; a typical pair of outer stamens (OS_1 and OS_2) are between an outer tepal (OT) and the gynoeceum, which has a dorsal (D) indicated ($40\times$). B) Longitudinal section cut peripherally and perpendicular to an outer supply radius; in the upper area, two outer stamen (OS_1 and OS_2) bundles are divergently departing, whereas in the lower area, the clustered outer tepal supply occurs, that is, the OTM and the OTL pair ($40\times$). C) Cross-section showing the typical outer tepal-stamen vascularization; section below that in A, and through the midreceptacle; the intercarpellary gland is prominent; the typical pair of outer stamen (OS_1 and OS_2) bundles is along the same radii as the outer tepal laterals

Tepals and Their Vascularization

The linear to linear-lanceolate tepals of the two whorls are distinct and subequal. The three outer tepals are slightly wider than those of the inner cycle. The outer tepals have an average length of 1.5 cm (range: 1.0–1.7 cm) and an average width of 3.2 mm (range: 2.5–4.0 mm), whereas the inner tepals have an average length of 1.5 cm (range: 0.9–1.6 cm) and an average width of 2.7 mm (range: 2.0–3.7 mm). In flower the inner tepal surfaces are a whitish yellow centrally and dull green along the margins. The outer tepal surface is a dull yellowish white. The tepals persist into the fruiting stage and undergo a color change to a brown. There is no tepal perigyny within either cycle. There is however a limited degree of stamen epitepaly (Figs. 2, 6, 7).

Basally each tepal receives three bundles—two laterals and a median. The outer tepal vasculature is established as three division bundles move outwards. Each is derived directly from a single pedicel ring bundle. The two bundles, which determine the outer tepal laterals (OTL), each undergo two successive divisions. These additional divisions establish besides the outer tepal laterals (OTL), the outer stamen traces (OS), and the ventral supply (V) (Figs. 6 D–H; 7 D–H; 8; 9). The pedicel ring bundle, which establishes via a division the outer tepal median (OTM), on the other hand, normally undergoes a single division, which results in the formation of the outer tepal median (OTM) and the dorsal (D) (Figs. 4 A, C–E; 6 D–H; 7 D–H; 8; 9). If there were two divisions in this later parental pedicel bundle, an additional stamen trace would be formed, thus giving a stamen number greater than the typical nine (Figs. 4 D; 9).

The origin of the inner tepal vasculature is similar to that observed for the outer tepals (Figs. 4 B, E–F; 8; 9). Basally each inner tepal receives two laterals (ITL) and a median (ITM). The two laterals per tepal arise directly from bundles in the pedicel ring and do not undergo any receptacle division (Figs. 4 E–F; 8). The bundle, which supplies the inner tepal median, on the other hand, does undergo a single di-

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(OTL), whereas the outer tepal median (OTM) shares a common radius with the dorsal (D) (50×). D) Cross-section showing the atypical outer tepal-stamen vascularization; section level similar to C, but from a different flower; three outer stamen (OS₁–OS₃) bundles are associated with the three outer tepal bundles; a dorsal (D) indicated; the additional outer stamen (OS₂), which is along the OTM-D radius contributes to the greater than nine total stamen configuration (50×). E) Cross-section showing the typical inner tepal-stamen vascularization; the branch bundle that becomes the inner stamen (IS) trace is along the same radius as the inner tepal median (ITM); two inner tepal laterals (ITL) are present (50×). F) Longitudinal section cut peripherally and perpendicular to an inner supply radius; the inner stamen (IS) bundle is in the same vertical plane as the inner tepal median (ITM) (35×).

vision, and the resulting innermost product of this division functions directly as the inner stamen trace (IS) (Fig. 4 F).

Occasionally, there are additional laminal divisions within the tepal laterals. These divisions involve both the outer tepal laterals (OTL) and the inner tepal laterals (ITL), and result in five veins (traces) within the tepals. When this condition occurs, the higher vein numbers are usually observed only near the base of the freed tepals. The veins are parallel within the laminal tepal surface of both whorls, and there is no cross-connection between them.

Stamen Number, Morphology, and Vascularization

The stamen number of nine for *Pleea* has historically been used to isolate this monotypic genus from the typical six stamen lilies. Within the artificial Linnean system, *Pleea* was placed in the Enneandria (nine stamens) class and the Trigynia order (Michaux, 1803; Sims, 1818). Redouté's illustration (t. 25), which accompanied the type description (Michaux, 1803), shows three open flowers each with nine stamens. Sims' illustration (t. 1956) for *Curtis' Botanical Magazine* (1818) shows two open flowers with 10 stamens each, and adds that "the stamens are by no means confined to the number nine, but seems to vary from six to twelve. The laciniae of the corolla are constantly six, perhaps, therefore the number twelve may be the most natural for the stamens, though most generally reduced below that number by abortion." This was the first report of a stamen number other than nine for *Pleea*.

Endlicher (1840) stated that the stamen number was nine with a pair of stamens in front of each outer tepal, that is, *ante sepala exteriora gemina*. Both Kunth (1843) and Baker (1879) reported the stamen number as varying between nine and 12, whereas Engler (1888) and Krause (1930), on the other hand, stated that the stamen number varied between six and 12, but that the total stamen number was usually nine with a pair of stamens in front of each outer tepal.

A stamen count of 200 flowers from 47 different individuals (herbarium specimens) selected from throughout the range gave the following stamen number distribution: six—0; seven—0; eight—0; nine—189 (94.5%); 11—0; 12—0. Of the 30 flowers embedded and sectioned for anatomical examination, 28 had nine stamens and two had 10 stamens. Clearly the lower numbered stamen classes, that is six through eight, are rare or nonexistent, as are the higher numbered stamen classes, that is, 11 and 12.

In the normal nine stamen flowers (Fig. 2), the original observations of Endlicher (1840) were confirmed. There are two stamens in front of each outer tepal and a single stamen in front of each inner tepal. This configuration gives a total of nine stamens. When a tenth stamen is present, it is associated with an outer tepal and the pair of stamens

already present. There are three stamens in front of one outer tepal, two stamens in front of two outer tepals and a single stamen in front of each of the three inner tepals, which gives the total of 10 stamens. Theoretically, it would be possible to have 12 stamens arranged in the following fashion—three stamens associated with each outer tepal (nine) and a single stamen associated with each inner tepal (three). An inaccurate sketch of a *Pleea* flower with 12 stamens was presented by Small (1933). It shows a partial floral sketch with a single stamen in front of an outer tepal, a single stamen in front of an inner tepal and a single stamen between the outer and inner tepal.

The stamens of both the outer whorl and the inner whorl are equal. Both whorls are freed directly within a short vertical distance from the gynoecial base, although there is a limited degree of stamen adnation to both tepal whorls. The glabrous filaments are dilated basally, filiform terminally, and divergent at anthesis. Each filament contains a single vein (trace). The average free filament length for the filaments from both whorls is 4.45 mm (range: 4.2–5.2 mm). The three anthers of the two whorls are equal, basally divided, laterally dehiscent, and versatile. The average anther length is 2.69 mm (range: 2.4–3.0 mm). Each anther sac is bilocular and the walls of the endothecial cells are lined with banded thickenings.

The vascularization of the outer stamens differs from that of the inner stamens. The outer stamen vascularization is associated with the bundles supplying the outer tepal laterals of the outer tepals. Each pedicel ring bundle, which branched to form an outer tepal lateral (OTL), continues vertically for a short distance and then divides. The outermost division product becomes the outer stamen trace (OS) (Figs. 4 A–C; 6 E–H; 7 E–H; 8; 9). The two pedicel bundles, which supply the two outer tepal laterals (OTL), also supply the two outer stamen (OS) traces.

The single inner stamen (IS) trace is derived from the continuing bundle that remains following the formation of the inner tepal median (ITM) (Figs. 4 E–F; 6 E–F; 7 E–F; 8; 9). The three single inner stamen traces of the flower are therefore along the inner tepal median (ITM)—septal radii. Each of the outer stamens (OS) within the three outer pairs, on the other hand, is 30° from the outer tepal median (OMM)—dorsal (D) radii. Summary diagrams show the patterns of stamen vascularization (Figs. 6–9) for the typical nine stamen configuration.

The derivation of the tenth (or additional) stamen is from the outer tepal median supplying bundle, and not as one might guess from the inner tepal vasculature. The tenth (or additional stamen) is derived from an additional division and departing branch from the bundle, which supplies both the outer tepal median (OTM) and the dorsal (D) (Figs. 4 D; 9 A). The net result is three stamens associated with the

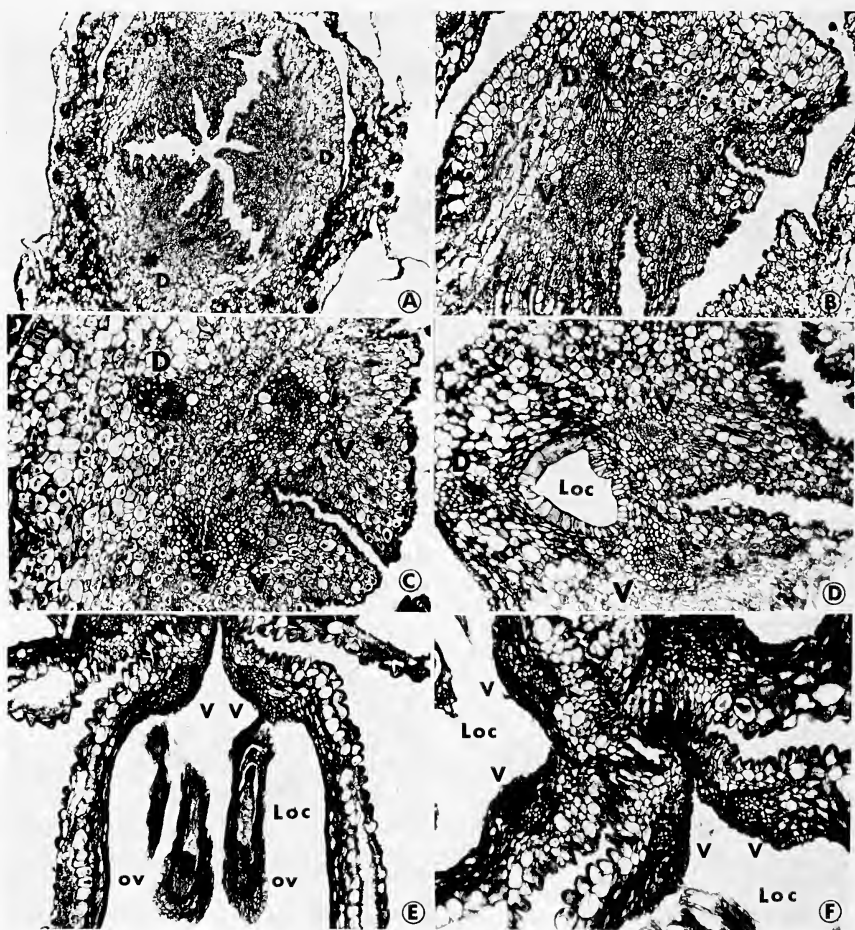


Fig. 5.—Serial cross-sections through the gynoecium of *Tofieldia tenuifolia* (Michx.) Utech. A) Tepals and stamens cut off from the gynoecium; the central intercarpellary gland is broadly six armed; the three larger arms are along the septal radii, whereas the three smaller arms are along the dorsal (D) radii (25 \times). B) Section above A in which a stipitate carpel is freed via the external connections along the septal radii of the intercarpellary gland; dorsal (D) and ventrals (V) indicated (30 \times). C) Similar section to B, but emphasis is on the smaller, dorsal radius arm; dorsal (D) and ventrals (V) indicated (30 \times). D) Stipitate carpel section above C showing the internal locular (Loc) opening; the cells of the locular wall differ from those which line the intercarpellary gland; dorsal (D) and two ventrals (V) indicated (30 \times). E) Section through the mid-gynoecium; within the locule (Loc) there are two horizontally orientated ovules (ov), one of which clearly shows the bitegmic condition; the two ventrals (V) of the carpel are located along the inrolled septal wing tips (40 \times). F) Upper gynoecium showing the interdigitating papillae of the stigmatoid support system along the septal radii; ventral (V) supplies for two locules (Loc) indicated (40 \times).

outer tepal. One is along the OTM-D radius, this is the additional one, and there are two typical stamens each located ca. 15° on either side of the OTM-D radius. In the 30 sectioned flowers, there was never an indication of additional stamen vasculature associated with or derived from bundles supplying the inner tepal laterals (ITL).

The pattern of stamen and tepal vascularization in *Pleea* parallels that in *Tofieldia*, but not *Nartheceum*. An examination of several species of *Tofieldia* (*T. calyculata* (L.) Wahlenb., *T. racemosa* (Walt.) BSP, *T. glabra* Nutt., *T. coccinea* J. Rich., *T. japonica* Miq., *T. glutinosa* (Michx.) Pers.) indicates a reduction series in this genus for the number of tepal bundles. Two examples are provided in Fig. 9 (C–D) for *Tofieldia*, while sketches A and B are for the 10 (or additional) stamen and nine stamen configurations, respectively. This sequence does not directly imply a phylogenetic arrangement of *Pleea* and members of *Tofieldia*, but rather an anatomical reduction series relating the outer tepal and outer stamen vasculature. A similar type of pedicel ring configuration occurs in both *Pleea* and *Tofieldia*, as well as a similar type of division within these bundles to form the various types of tepal and stamen traces.

Three outer stamens is the rule within the genus *Tofieldia*. However there is a reduction series in the number of veins (bundles) in the outer tepals. Three veins (Fig. 9 C) is the most common type, but outer tepals with a single median also occur (Fig. 9 D). The pattern in *Tofieldia* with three outer tepal bundles and a single outer stamen (Fig. 9 C) is identical to the pattern of the inner tepal and stamen in *Pleea* (Figs. 4 E–F; 6 E–H; 7 E–H; 8).

In the genus *Nartheceum* there are consistently six stamens, and the outer and inner stamen bundles have a fusion origin which is totally unlike that observed in *Pleea* and *Tofieldia* (Utech, unpublished manuscript). The bundles are also bifid throughout most of the filament length. Both *Pleea* and *Tofieldia* have 2-sulcate pollen grains, whereas those in *Nartheceum* are 1-sulcate (Erdtman, 1966).

Gynoecium Morphology and Vascularization

The obovoid to elliptic, tricarpellate gynoecium in *Pleea* exhibits several primitive liliaceous characteristics. Basally the three carpels are free and have vascularized stipes (Figs. 5 B–D; 6 H–J; 7 H–J). This stipitate region is associated with an intercarpellary gland that originates in the upper pedicel's pith. Because the outer adjoining septal surfaces are only appressed with papillae that interdigitate, there is no carpel fusion throughout the vertical height of the gynoecium. In fruit the leathery carpel walls show no indications of true dehiscence, though most floras indicate septicidal dehiscence. Actually the carpels do separate along the septal radii, but this is due to pulling apart of

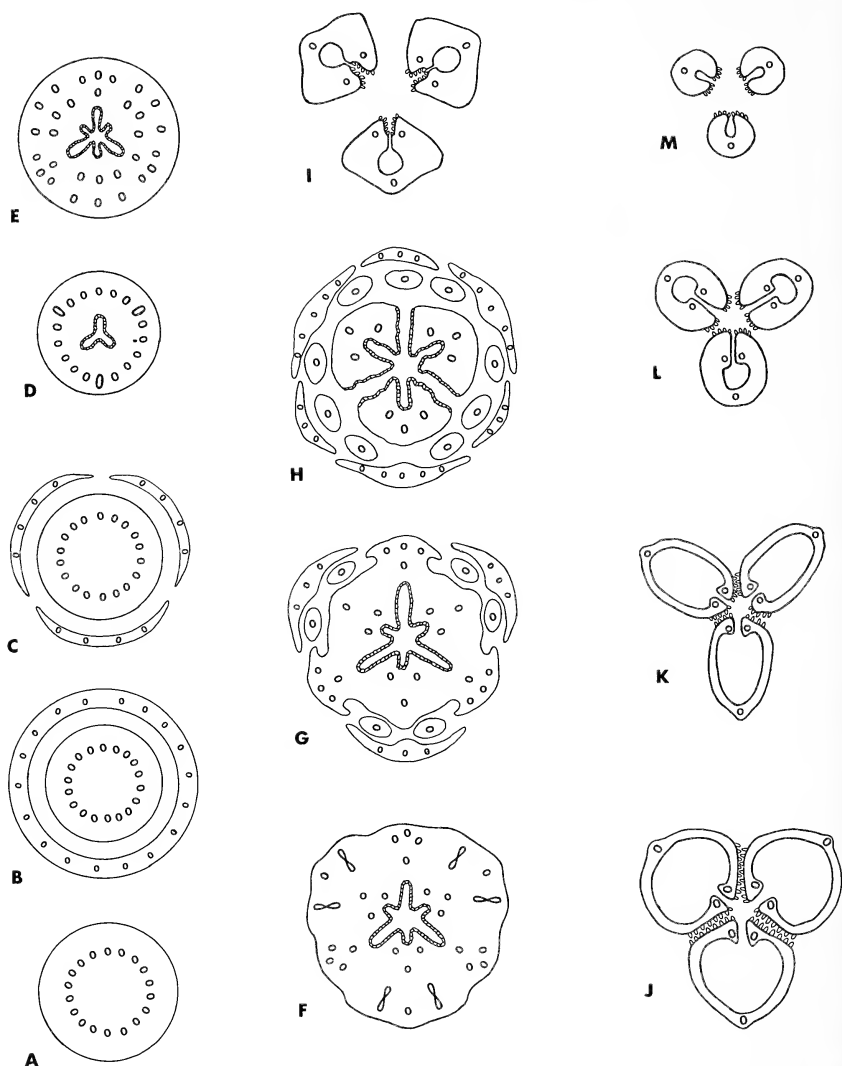


Fig. 6.—Serial cross-sections of *Tofieldia tenuifolia* (Michx.) Utech. A) Lower pedicel below the bracteoles with a ring of 18 vascular bundles, this section as well as B and C are surrounded by the bract. B) Mid-pedicel showing the connate bracteole with a 18-bundled vascular configuration, the pedicel also has a 18-bundled configuration. C) Upper pedicel with 18 bundles surrounded by the three freed bracteole blades, each blade has a reduced number, four, of bundles. D) Upper pedicel below the receptacle, three of the 18 bundles depart along the yet undefined dorsal radii, triwedged cavity in the center is the opening of the intercarpellary gland, gland lined with secretory cells. E) Receptacle base with the intercarpellary gland exhibiting six wedges, that is, the three larger along the septal radii and the three smaller along the dorsal radii; 12 of the 18

the interdigitating papillae along the septal walls. The style and stigma of each carpel are free.

The intercarpellary gland (Gl) in *Pleea* originates as an irregular cavity in the central pith region of the upper pedicel (Figs. 3 E–F; 6 H–I; 7 H–I). From the base of this cavity, it is lined by a single layer of intercarpellary papillae. The papilloid cells stain darker than those in the surrounding pith and probably have a secretory function (necrotic). The gland cavity enlarges further up the floral axis; first along the three, yet undefined septal radii, and then along the dorsal radii (Figs. 3 F; 5 A; 6 D–G; 7 D–G). The gland is six armed, at this receptacular level. As the tepals and stamens are freed, the bases of the three carpels are also freed along the gland's septal radii, creating the freed stipes of the three carpels. Also at this level, the intercarpellary papillae extend along the septal radii of the periphery of each carpel. The level of gland opening is below the level at which the locules open. The gland's external opening is continuous with the three septal grooves that continue up the sides of the gynoecium.

In *Pleea*, the basal stipes of each freed carpel have three bundles—a dorsal (D) and two ventrals (V) (Figs. 5 B–D; 6 H–I; 7 H–I). The epidermis of the stipes is differentiated from the septal and central

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original bundles have divided and their branch bundles are along shared radii, nine of the 12 divided bundles, that is, three sets of six bundles will with further division and orientation establish the dorsal and ventral vasculature, as well as the supply for the six outer stamens and the outer tepals, where the remaining three of 12 divided bundles, that is, three bundle pairs will establish the three inner stamens and the supply of the inner tepals. F) Receptacle base showing further bundle division and movement; three sets of three bundles have moved inwards to establish dorsal and two ventrals per set, the tepal medians of both the outer and inner whorls are established, as are the inner tepal laterals, the bundles lateral to the outer tepal medians are dividing to form the two outer tepal laterals and the two outer stamen bundles; intercarpellary gland increases in internal area. G) Outer tepals with three traces and the outer paired stamens cut off from the receptacle, the outer stamen traces have a shared origin with the outer tepal laterals; the inner tepals, also with three traces, and the unpaired inner stamen are not yet cut off. H) All tepals and stamens freed from receptacle-gynoecium; the nine stamen condition is typical; additional divisions have occurred within the outer tepals; three stipitate carpels are formed as the intercarpellary gland is freed to the outside along the septal radii, each carpel has a dorsal flanked by two laterals; the intercarpellary gland is lined with secretory cells at this level. I) Three stipitate carpels with locules and positioned vasculature; the stamens and tepals not shown; a second cell type replaces the secretory cells along the central floral axis. J) Midcarpellary section showing the interdigitating papillae along the septal wings, the septal wings are not fused; ovule supply occurs at this level, but ovules are not indicated; a unilocular relationship exists between the three carpels. K–M) Transition from the upper carpellary zone to the three freed styles; the three dorsals terminate slightly below the stigmas; a hollow pollen path lined with papilloid-stigmatoid cells coincides with the central floral axis.

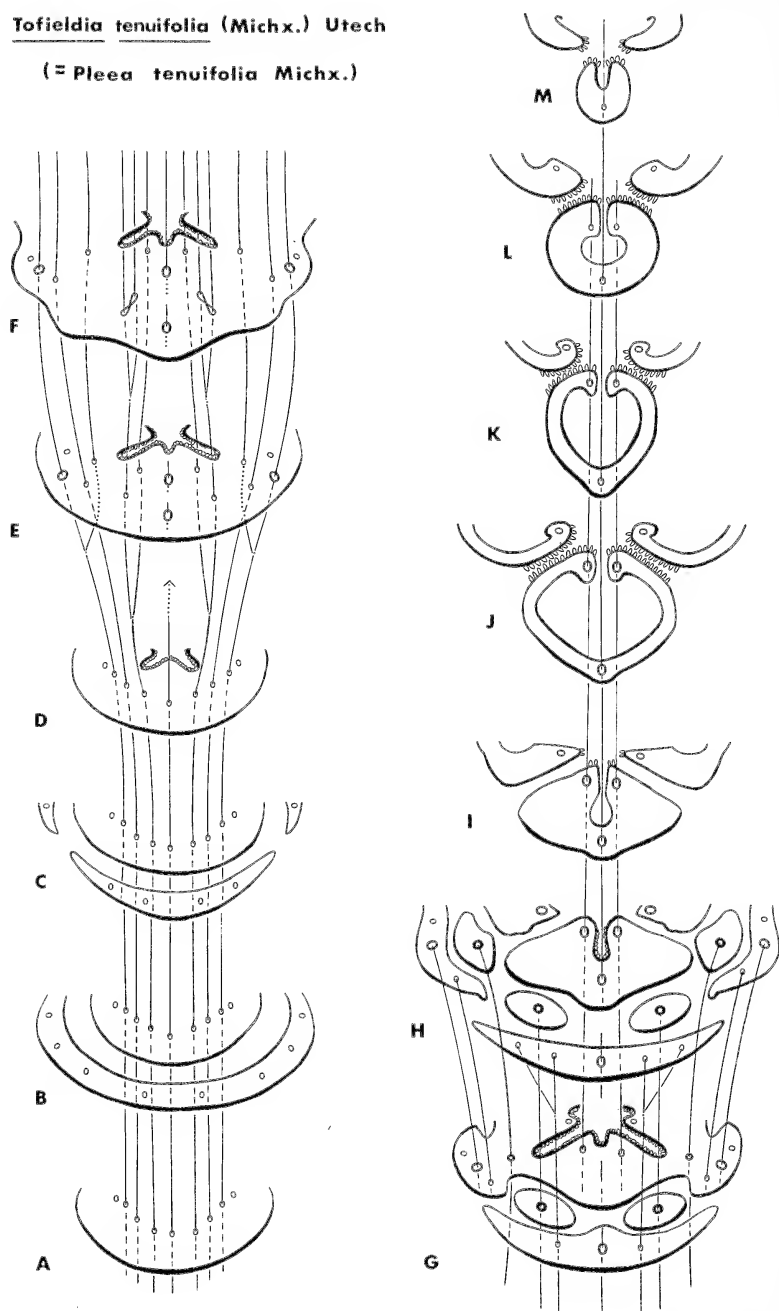
Tofieldia tenuifolia (Michx.) Utech(*= Pleea tenuifolia* Michx.)

Fig. 7.—Projected cross-sections of *Tofieldia tenuifolia* (Michx.) Utech. Lettered sections correspond to those in Fig. 6.

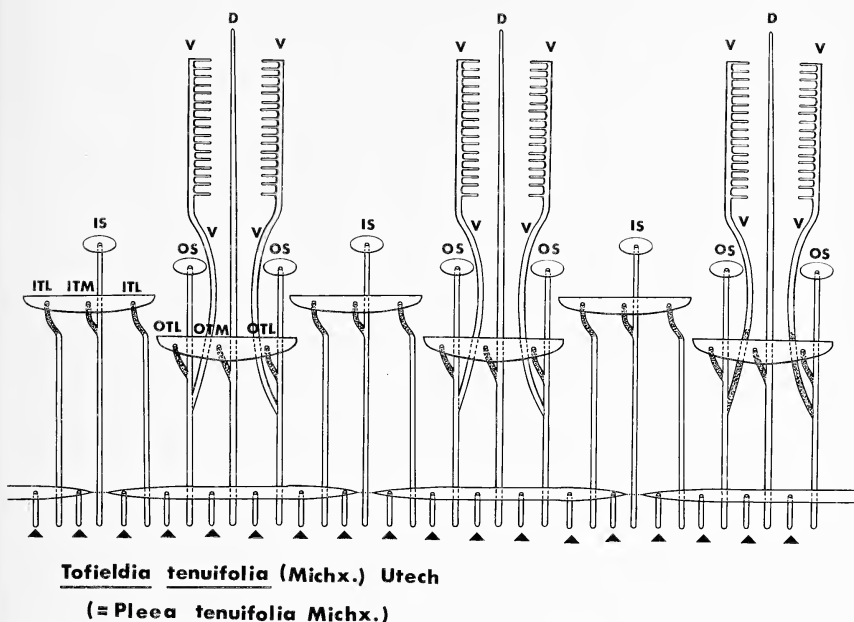


Fig. 8.—Longitudinal summary roll-out diagram of *Tofieldia tenuifolia* (Michx.) Utech showing the vascularization of the three basally connate bracteoles, the tepals and stamens, and the gynoecium. The following, text introduced, code applies to the various bundles: OTL = outer tepal lateral, OTM = outer tepal median, ITL = inner tepal lateral, ITM = inner tepal median, OS = outer stamen, IS = inner stamen, D = dorsal, V = ventral, and F = funicular trace. Only one set of the outer and the inner tepals have their vasculature labeled.

facies which consist of papilloid cells. Along the central (inner) facies of the stipes, there are internal gland indentations along the dorsal radii, but these indentations are not basally connected with the locules of the carpels. There is no basal connection between the intercarpellary gland (GI) and the locules (Loc). The locules (Loc) appear centrally within the broadening stipes.

Above the stipe region, a more elongated type of papilloid cell occurs along the central axis and the outer surfaces of the septal wings. This second type of papilloid cell replaces those that are characteristic of the basal intercarpellary gland (GI). The locules (Loc) open at this level along the dorsal radii and the central axis. The three locules are subsequently confluent. The resulting compound gynoecium is therefore unilocular from a region just above the stipes, though the degree of lateral "fusion" of the adjoining septal wings is limited to the appressed, interdigitating papillae.

The inner septal wing tips are recurved (inrolled) into the locules. Each wing tip has a single ventral (V), which is reversed, that is, the phloem is adaxial and the xylem is abaxial, and this bundle reversal is associated with the septal tip being inrolled. From each ventral (V), a vertical series of funicular (F) branches arise (Figs. 4 E; 6 I-L; 7 I-L). There are usually 18 bitegmic ovules associated with each ventral (V) (Fig. 8), or 36 ovules per carpel. Terminally there is no cross-connection between the dorsal (D) and ventral (V) supplies.

There is no abrupt transition from the upper gynoecial regions to the three free styles (Figs. 6 L-M; 7 L-M). Papillae line the open central axis of the upper gynoecium and these papillae are also continuous along the adaxial stylar surface. The dorsals (D) are presented in the styles, the ventrals are not. Throughout the ovary, there is no branching of the dorsals. Also there are no septal axials in *Pleea*. Raphides were not observed.

The ovules in *Pleea* are bitegmic with their long embryo sac axes in a horizontal plane, and parallel to the dorsal radii (Fig. 5 F). The ovule orientation is best described as pleurotropous (terminology after Björnstad, 1970). The micropyles are directed towards the central axis and the open, intercarpellary papillae. There are two rows of ovules per carpel with each row supplied from different sides of the inrolled carpel margins. There are usually 18 ovules per row, that is, 36 ovules per carpel (Fig. 8). The funicular traces (F) and their stalk are also parallel to the dorsal radii, because lengthwise fusion has occurred between the funicular stalk and the adjacent outer integument. A short, distal appendage in the horizontal plane occurs at the chalazal end of each ovule. The appendage length increases following anthesis.

The brown, glabrous seeds are distally appendaged (Fig. 2). The clear appendage is thin and elongate (1.7-2.5 mm) and is attached at a slight angle to the seed proper. The seed is usually between 1.1 to 1.5 mm long. The horizontal seed packing is similar to that of the ovules. The seed appendages from one vertical carpellary row are directed horizontally into the locular space on the other side of the carpel. The appendages from the other vertical carpellary row are directed in criss-cross fashion to the opposite side of the locule. The criss-crossed appendages of the two seed rows can be seen in cleared mature fruits. The seed appendages in *Pleea*, as well as the packing of the seeds, are similar to those in many species of *Tofieldia* (Gleason, 1952; Hitchcock, 1944; Ohwi, 1965; Kitamura et al., 1965).

The independent stipitate carpels, the basal intercarpellary gland, and the lack of septal wall fusion, which characterize the gynoecial morphology of *Pleea*, are distinctive characters within the primitive subfamily Melanthioideae, but are not exclusively observed in *Pleea*. Similar carpel morphology and vascular anatomy occur in the genus

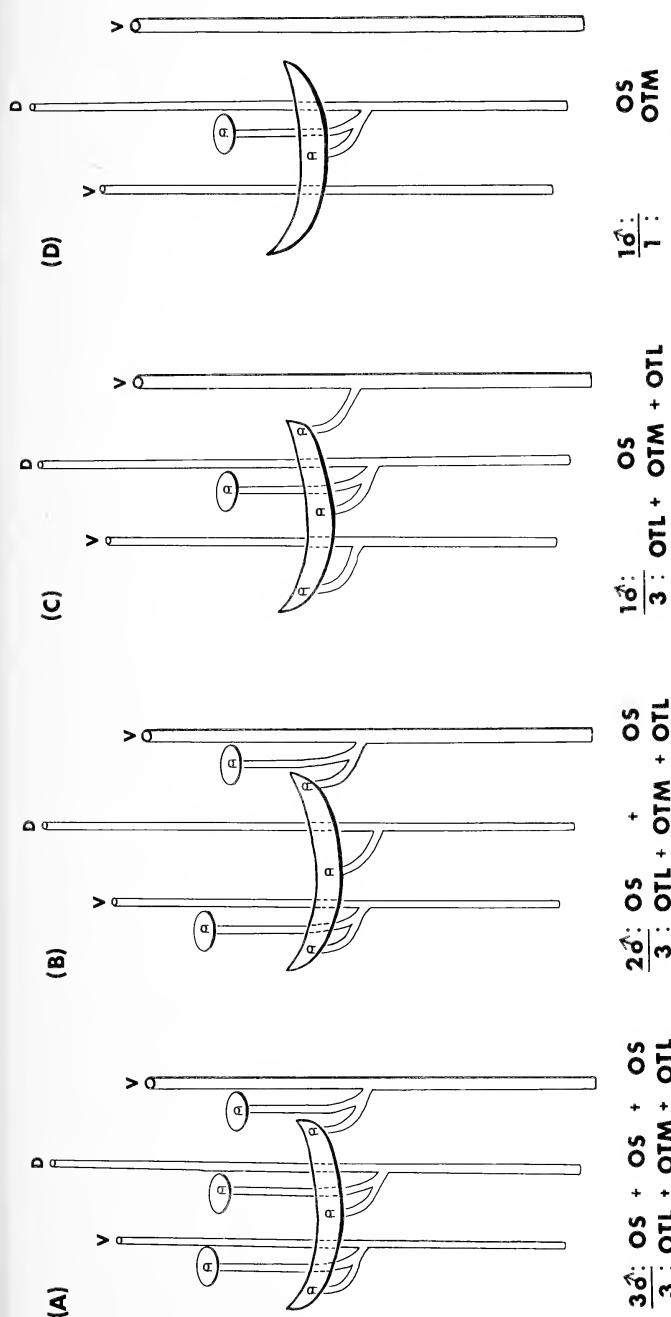


Fig. 9.—Comparative reduction series in *Tofieldia* diagrammed to show the different vascularization configurations within the outer tepals and outer stamens. Below each inset figure, there is a summary code: OS = outer stamen, OTL = outer tepal lateral, OTM = outer tepal median, D = dorsal, and V = ventral. A) *T. tenuifolia* with three outer tepal bundles and three outer stamen bundles; this outer configuration results in the rare 10, 11 or 12 total stamen number; cf. Fig. 4 D. B) *T. tenuifolia* with three outer tepal bundles and two outer stamen bundles; the latter share a common origin with the outer tepal laterals; this outer pattern results in the typical nine stamen configuration; cf. Figs. 2 F, H; 4 B–C. C) Representative example, *T. racemosa* with three outer tepal bundles and a single outer stamen bundle; cf. Fig. 10; if the continuing dorsal (D) and the two ventrals (V) were excluded, this pattern would approximate that of the inner tepals and inner stamens of *T. tenuifolia*. D) Representative example, *T. calyculata* with a single outer tepal bundle and a single outer stamen bundle; cf. Fig. 11, and Leinfellner (1962a, 1962b, 1963) for additional reductions.

Table 1.—*Generic comparison of the Englerian Tofieldiaceae: Pleea, Tofieldia and Narthecium.*

Character	Genus		
	<i>Pleea</i> Michx.	<i>Tofieldia</i> Huds.	<i>Narthecium</i> Moehr.
Distribution	Southeastern U.S.; coastal plain; cf. Fig. 1	North temperate and circumpolar zones with outliers in the mts. of South America	East and west U.S.; Europe; East Asia; highly disjunct within temperate zone
Number of species	1; this paper	ca. 15-20; highly variable	ca. 4-5; very similar
Habit	Rhizomatous perennial with equitant leaves	Rhizomatous perennial with equitant leaves	Rhizomatous perennial with two-ranked leaves
Inflorescence	Simple raceme, few flowered, one flower per node	Simple to compound raceme, few to many flowered, one to three flowers per node	Simple, dense raceme, many flowered
Bract	Yes; large, ensheathing, aristate tipped	Yes; size variable	Yes; small, linear
Bracteoles	Yes; three-parted, basally connate, cf. Fig. 2	Yes and no; some groups with and some without; if present, three-parted	Yes; small, linear
Tepal vascularization			
Outer cycle of three	Constantly three-bundled	One to three bundled	Constantly three-bundled
OTM	One; simple, single branch bundle	One; simple, single branch bundle	One; fusion product
OTL	Two; simple, single branch bundles	Zero to two; if present, then simple, single branch bundles	Two; simple, single radial branch bundles

Table 1.—(Continued)

Character	Genus		
	<i>Pilea</i> Michx.	<i>Tofieldia</i> Huds.	<i>Narthecium</i> Moench.
Inner cycle of three	Constantly three-bundled	One to three bundled	Constantly three-bundled
ITM	One; simple, single branch bundle	One; simple, single branch bundle	One; fusion product
ITL	Two; simple, single branch bundles; cf. Figs. 6-9	Zero to two; if present, then simple, single branch bundles; cf. Figs. 10-11	Two; simple, single radial branch bundles; cf. Fig. 12
Pedicel vascularization	c. 18 ring bundles; cells of cortex unlike pith; surrounding sclerenchymatous sheath present; cf. Figs. 6-9	c. 18 ring bundles; cells of cortex unlike pith; surrounding sclerenchymatous sheath present; cf. Figs. 10-11	Three- and 12-bundled configurations; cells of cortex similar to pith; surrounding sclerenchymatous sheath absent
Intercarpellary gland (Gl)	Yes; basal origin in pedicel; nectiferous; cf. Figs. 6-9	Yes; basal origin in pedicel nectiferous; cf. Figs. 10-11	No; cf. Fig. 12
Stamen number, vascularization and morphology	Usually nine; rarely 10 or more	Usually six, but variable (cf. Leinfellner, 1962a, 1962b, 1963)	Usually six
OS and IS	Simple, single branch bundle; cf. Figs. 6-9	Simple, single branch bundle; cf. Figs. 10-11	Bifid, fusion product; cf. Fig. 12
Anthers	Introrse, versatile, laterally dehiscent	Introrse, versatile, laterally dehiscent	Introrse, versatile, laterally dehiscent
Filaments	Dilated basally, glabrous; cf. Figs. 6-9	Dilated basally, glabrous; cf. Figs. 10-11	Ovoid basally, pubescent; cf. Fig. 12

Table 1.—(Continued)

Character	Genus	
	<i>Pilea</i> Michx.	<i>Tofieldia</i> Huds. <i>Narthecium</i> Moehr.
Gynoecium		
Carpel vascularization		
Dorsal	Simple, single branch bundle	Simple, single branch bundle
Ventral	Simple vertical with many horizontally derived funicular branches; cf. Figs. 6-9	Simple vertical with many horizontally derived funicular branches; cf. Figs. 10-11
Carpel morphology		
	Ovary stipitate, basally apocarpous	Ovary stipitate, basally apocarpous
	Septal wing tips free and loculicidally inrolled	Septal wing tips free and loculicidally inrolled
	Septicidally separated; cf. Figs. 6-9	Septicidally separated; cf. Figs. 10-11
	Distally appendaged seeds; cf. Fig. 2	Distally appendaged seeds
Seed morphology		
		Septicidally separated; loculicidally dehiscent
		Distally and proximally appendaged seeds
		Fusion product
		Numerous vertically parallel ventrals each with a one to one funicular correspondence; cf. Fig. 12
		Ovary non-stipitate, sessile; basal placenta massive
		Septal wing tips fused basally, free upper ovary and not inrolled
		Dorsal grooves present; loculicidally dehiscent
		Distally and proximally appendaged seeds

Tofieldia (Figs. 10–11; Anderson, 1940; El-Hamidi, 1952; Table 1). These characters on the other hand are not found in the genus *Nartheceum* (Fig. 12; Table 1; Utech, unpublished manuscript). *Tofieldia* and *Nartheceum* are tribal (Tofieldieae) cohorts with *Pleea*.

SUMMARY

Immediately following this summary of the vascular floral anatomy and carpel morphology of *Pleea tenuifolia* is a discussion and table (Table 1), which compares these aspects of *Pleea* to those in both *Tofieldia* and *Nartheceum*.

The inflorescence of *Pleea* is a simple raceme with three to eight flowers. An elongate ensheathing bract with an aristate tip is associated with each pedicel. Basally the pedicel has an axial system of 18 bundles which are continuous to the base of the receptacle. At midpedicel length, a three lobed, basally connate bracteole tube is observed. Although 18 bundles enter the connate base, only several reach the three freed subsections.

Each of the 18 pedicel bundles contributes a branch bundle to the tepal supply. Nine are associated both in the outer and inner tepal whorls. Each of the three outer tepals has an outer tepal median (OTM) and two adjoining laterals (OTL). Likewise, each of the three inner tepals has an inner tepal median (ITM) and two laterals (ITL).

The usual stamen number is nine with two outer stamens per each outer tepal (six) and a single inner stamen per each inner tepal (three). The bundles for the outer stamens (OS) are derived via branches from the same pedicel ring bundles which established the outer tepal laterals (OTL). If an additional stamen were present, for example a tenth, it would occur through a division of the pedicel ring bundle that established the outer tepal median (OTM). The three inner stamens (IS) are derived from those pedicel bundles which established the three inner tepal medians (ITM).

The remaining portions of those pedicel ring bundles, which supplied the outer tepals (OTL + OTM + OTL) and the outer stamens (OS), establish the gynoeceal vasculature. Three independent stipes characterize the base of the tricarpellate gynoeceum in *Pleea*. Each stipe has three bundles, a dorsal (D) and two ventrals (V). The dorsal (D) is continuous via previous divisions at lower levels with the outer tepal median and their shared common pedicel bundle. The two ventrals (V) per stipe are continuous at a lower level with the supplies of the outer tepal laterals (OTL) and the outer stamens traces (OS) and the associated pedicel bundles.

The two ventrals (V) of each carpel have funicular branches (F) from each side of the locule. Therefore, there are two rows of ovules per

locule. There is no interconnection between the dorsal and ventral supplies. Only the dorsals occur in the styler regions.

DISCUSSION AND CONCLUDING REMARKS

The present study has established several previously unknown facts about the carpel morphology of *Pleea tenuifolia*. At the level at which the tepals and stamens are freed, the gynoeceum base is divided into three vascularized stipes. Free stipitate carpels are rare in the Liliaceae *sensu lato* (Gates, 1918; Eames, 1961; Anderson, 1940; Brown, 1938). Stipitate carpels are, however, known in *Tofieldia*. Anderson (1940) presented both cross-sectional and longitudinal views of the basal stipes of *Tofieldia racemosa* (Fig. 10 B, E), whereas a complete series of cross-sections for *T. calyculata* by El-Hamidi (1952) shows the basal origins of the stipes (Fig. 11 K-N). Additional personal observations of *T. glutinosa*, *T. glabra*, *T. coccinea*, and *T. japonica* have confirmed the presence of stipes throughout the genus. The morphology and vascularization of the stipitate carpels in *Tofieldia* are identical to those reported here for *Pleea* (Figs. 5 B-D; 6; 7). There are no stipitate carpel bases in *Narthecium* (Fig. 12; Table 1).

In *Pleea*, there is an intercarpellary gland which originates centrally in the upper pedicel, and extends upwards between the freed stipes. This gland is lined with differentially stained papillae which probably function as secretory cells for the basal (nectary) gland. Basal carpellary glands (nectaries) are extremely rare in the Liliaceae (Eames, 1931, 1961; Anderson, 1940), and are only known in *Tofieldia* (Fig. 10, Anderson, 1940; Fig. 11, El-Hamidi, 1952). There are no basal intercarpellary glands in *Narthecium* (Fig. 12; Table 1).

There are two other kinds of nectaries, which are prevalent in the Liliaceae *sensu lato*, but only one of them involves a gynoeceal modification. These two types of functional nectaries are the tepal nectary and the septal (gland) nectary. The former is simply a basal, saccate tepal modification lined with secretory cells that serves directly as a nectary (Anderson, 1940; Utech and Kawano, 1976b, *Disporum sessile*; Utech and Kawano, 1978 *Heloniopsis orientalis*). The septal (gland) nectary, on the other hand, is formed by the incomplete lateral fusion of the outer septal wings (Anderson, 1940; Grassmann, 1884; Engler, 1888; Eames, 1931, 1961; Utech and Kawano, 1976a, *Maianthemum*; Utech, unpublished manuscript, *Smilacina*, *Polygonatum*). These nectaries are in the septal planes and their depth depends on the degree of septal wing fusion. The inner walls of these nectaries, that is, the lateral surfaces of the unfused septal wings, are lined with secretory cells, and usually have terminal openings in the upper carpellary styler regions.

Although these two kinds of nectaries are common within the Lili-

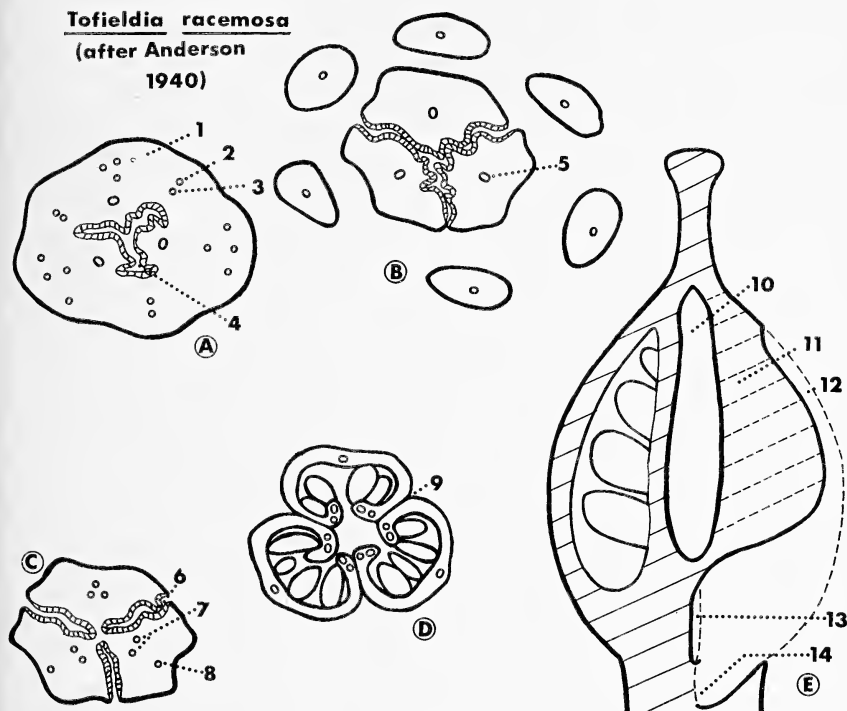


Fig. 10.—Cross-sections (A–D) and a longitudinal (E) view of *Tofieldia racemosa* (Walt.) BSP, redrawn from Anderson (1940; Plates VIa and VIII). A) Receptacle base showing the continuous, three-armed intercarpellary gland below the base of the stipitate carpels; the outer tepals with three bundles each and the inner tepals with a single bundle; common gynoeceal bundle per carpel (25×). B) Intercarpellary gland opening externally and subdividing the three carpels basally (apocarpous); stamens freed (25×). C) Disappearance of intercarpellary gland prior to locule opening; common gynoeceal bundle of each carpellary stipe divides to form carpel supply (25×). D) Midgynoeceum section showing inrolled septal wing tips (25×). E) Longitudinal section which shows the relationship between the basal intercarpellary gland, the hollow central axis, and the vertical plane through the appressed septum and opposing locule (30×). Number code: 1, Three outer tepal traces (OTL plus OTM plus OTL). 2, Single inner tepal trace (ITM). 3, Single inner stamen trace (IS). 4, Continuous basal intercarpellary gland lined with nectiferous cells. 5, Common stipitate carpel bundle. 6, External gland opening. 7, Ventral pair. 8, Dorsal. 9, Septal groove and radius of appressed septal margins. 10, Unilocular, intercarpellary space around the floral axis. 11, Septum (dotted lines). 12, Septal groove is continuous with the lower intercarpellary gland. 13, External gland opening and carpellary stipe zone. 14, Basal origin of intercarpellary gland.

aceae, usually they are mutually exclusive within a given species, that is, a given species may have one or the other type, but never both. Furthermore, the tepal and septal glands are characteristic of certain subfamilial and tribal associations (Anderson, 1940; Grassmann, 1884),

Tofieldia calyculata

(after El-Hamidi 1952)

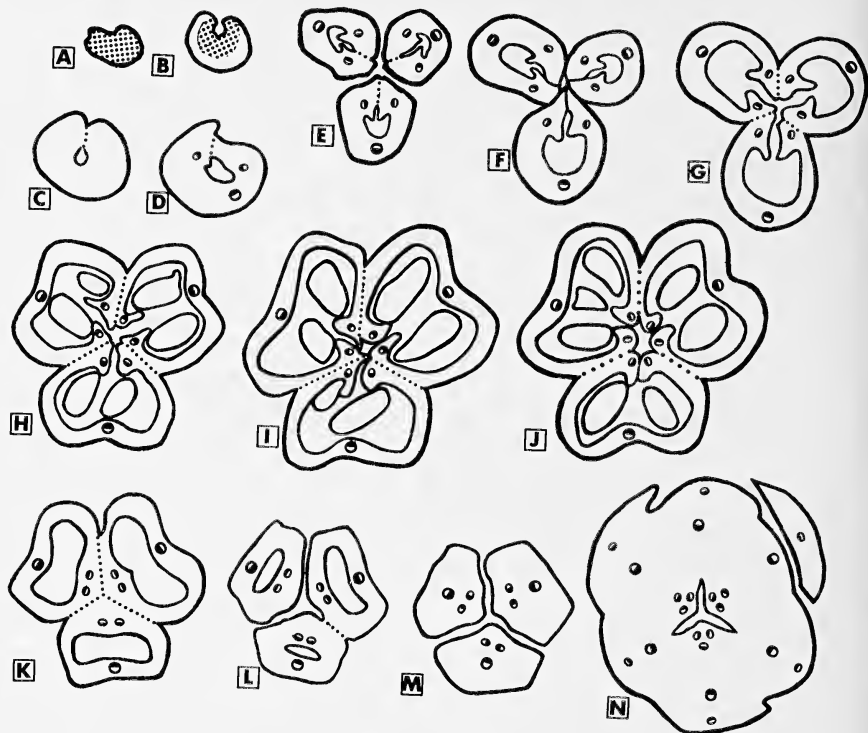


Fig. 11.—Serial cross-sections of *Tofieldia calyculata* (L.) Wahlenb. redrawn from El-Hamidi (1952; Fig. 1). A) Stigma with terminal stigmatoid tissue (35 \times). B) Stigma-style transition with stigmatoid tissue lining the styler opening (35 \times). C) Upper style showing the hollow styler canal; dotted line indicates the appressed inner septal margins; no vasculature present (35 \times). D) Lower style with a dorsal and two ventrals; inner septal margins appressed (35 \times). E) Upper gynoecium showing three free styles; the inner septal margins of each carpel inrolled into the upper locular space (30 \times). F) Similar to E, but from a lower section; the outer septal margins are appressed laterally (30 \times). G) Similar to F, but from a lower section; centrally the three carpels are free along the floral axis, that is, the gynoecium is unilocular; dotted lines indicate laterally appressed outer septal margins, whereas the inner septal margins are inrolled (30 \times). H) Upper gynoecium showing the upper ovule tier; inward ventral rotation corresponds to the inrolling of the inner septal margins (30 \times). I) Midgynoecium, similar to H (30 \times). J) Midgynoecium, similar to I (30 \times). K) Lower gynoecium with both the inner and outer septal margins appressed; section below level of ovule attachment; the two carpel ventrals are simple and ascend vertically with numerous horizontal funicular traces derived from them (30 \times). L) Opening of the three locules from within, this precedes both the lateral appression of the outer septal margins and the inrolling of the inner freed septal tips (30 \times). M) Three apocarpous stipes of the three carpels are due to the external openings of the intercarpellary gland; each stipe has a dorsal and two ventrals; tepals and stamens omitted (30 \times). N) Slightly oblique cross-section through the upper recep-

and express a common phylogenetic background. The joint occurrence in *Pleea* and *Tofieldia* of the rare basal intercarpellary (gland) nectary is therefore most significant.

In *Pleea* the three carpels are never fused along the vertical septal planes (Figs. 6, 7). Interdigitating papillae line these appressed facies, but there is never any septal fusion. The free inner septal tips (placenta) of each carpel are inrolled into the locules. The gynoeceium is therefore unilocular, because one locule is confluent with the other. Identical carpellary modifications were reported for *Tofieldia racemosa* (Anderson, 1940; Fig. 10) and *T. calyculata* (El-Hamidi, 1952: cf. Fig. 11; Klotsch, 1846; Leinfellner, 1962a, 1962b, 1963). In fruit, the carpels of both *Tofieldia* and *Pleea* are separated along the appressed, papillae-lined septal facies in a type of septicial dehiscence. Normal septicial dehiscence implies a fusion along the septa.

On the other hand, in *Nartheceum* (Fig. 12, Table 1; Utech, unpublished manuscript) a totally different carpellary structure exists. The lateral septal facies are completely fused throughout their vertical height. There are no septal (nectaries) glands. The septal wing tips (placenta) are large, not inrolled and fused basally. Dorsal grooves are associated with a carpellary weakened zone that in fruit results in loculicidal dehiscence.

Floral variability for the European *Tofieldia calyculata* was reported in detail by Leinfellner (1962a, 1962b, 1963). Variation in the number, morphology, and vasculature of the bracteoles, three bracteoles forming a *calyculus* are typical, the tepals, the stamens, and the carpels were illustrated and statistically recorded. Tepal to stamen, as well as stamen to carpel (gynostamen), transistional intermediates were discussed. That such variation occurs in *T. calyculata* further suggests that unreported homologous variation (Vavilov, 1951) occurs elsewhere within the genus, and that the atypical, but stabilized stamen number of nine presented here for *Pleea* may not be as unusual as first thought.

The allopatric pattern of range replacement between *Pleea* and *Tofieldia* along the southern Atlantic Coastal Plain is noteworthy. Neither *T. racemosa* (Walter) BSP nor *T. glabra* Nuttall, which occur in the same general area (Johnson, 1969; Radford et al., 1964) as *Pleea*, occupy the same sites. *Nartheceum americanum* Ker. is rare and found only in the pine barrens of the middle Atlantic Coastal Plain, and

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tacle; one of the three outer tepals is cut off; both the outer and inner tepals have a single trace, that is, a median; centrally the three dorsals and six ventrals are established around the continuous, three-armed intercarpellary gland (30×). Solid portion of each bundle represents the xylem elements.

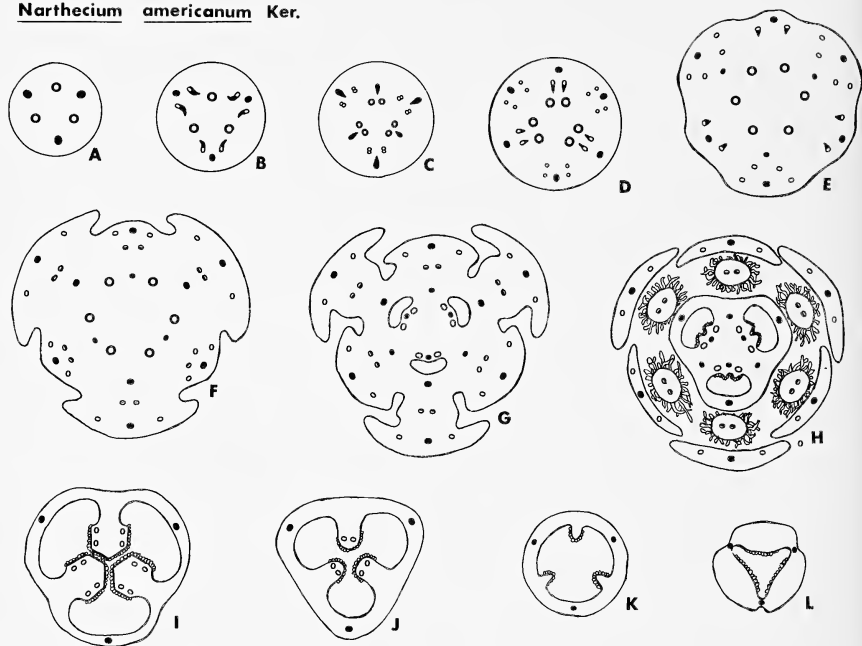
Nartheceum americanum Ker.

Fig. 12.—Cross-sectional series of *Nartheceum americanum* Ker. from the New Jersey pine-barrens (Utech 76-890 CM). A) Lower pedicel with the six-bundled configuration; solid outer bundles will establish the outer tepal medians (25 \times). B) Midpedicel with the 12-bundled configuration; a pair of branch bundles depart from each of the three compound inner bundles; each branch bundle is also compound (25 \times). C) Upper pedicel with further subdivision of the inner three bundles and the formation of a fusion bundle between each; the fusion bundles will establish the inner tepal medians (25 \times). D) Pedicel-receptacle transition zone with six central axial bundles and three fusion dorsals along the same radii as the outer tepal medians; an outer tepal lateral adjoins each median, as well as a pair of branch bundles which establishes the outer stamen supply (25 \times). E) Receptacle base with six large axial bundles, the three dorsals, and three new fusion bundles along the septal radii; the outer tepals peripherally defined (25 \times). F) Pedicel-receptacle base enlarged from section D, but with the same number of bundles (25 \times). G) Level of locular opening; epitepaly and staminal adnation occur within the outer cycles; a set of fusion bundles is formed between each pair of axial bundles along the dorsal radii within the central placenta (25 \times). H) Freed tepal and stamen cycles; paired bundles in each pubescent filament; two sets of fusion bundles present in the placenta, one set formed along the septal radii, the other along the dorsal radii; solid massive central placenta with obturators (25 \times). I) Midgynoeceum with the central placenta loculicidally divided and lined with stigmatoidal cells; compound ventrals subdivided into isolated ventrals which have a one to one correspondence with an associated funicular trace (25 \times). J) Upper unilocular gynoeceum; ventrals remain for upper ovule tier supply (25 \times). K) Upper gynoeceum-style transition with only the three dorsals present; stigmatoidal cells line the laterally fused, but reduced septal margins (25 \times). L) Style with three dorsals and opposing dorsal grooves; stigmatoidal cells line the hollow stylar canal (25 \times).

southward in the Blue Ridge Mountains of North Carolina (Small, 1924; Radford et al., 1964; Johnson, 1969). A parallel range shift from the northern pine barrens to the southern mountains also occurs within two other primitive lilies—*Xerophyllum asphodeloides* (L.) Nuttall (Wood, 1971; Utech, 1978a), and *Helonias bullata* L. (Utech, 1978b).

If the genus *Tofieldia* is viewed broadly, as it currently is, and the morphological and vascular variations in bracts, bracteoles and floral parts seen as homologous series of reductions, then *Pleea tenuifolia* must be considered a species of *Tofieldia*.

TAXONOMIC CONSIDERATION

Tofieldia tenuifolia* (Michaux) Utech, *comb. nov.

Pleea tenuifolia Michaux, Fl. Bor. Am. I: 247, t. 25. 1803.

Type presumably at Paris, but not seen. Description is such that no other species could have been meant. Type locality is wet forest margins in lower Carolina.

Rigid, subscapose, perennial herbs with stout rhizomes occurring in clumped clones. Leaves mostly basal, erect, evergreen, equitant, 1.0–3.5–(4.0) dm long, 1.5–4.0–(5.0) mm wide, bases auriculate, tips acute. Scapes stiff, (3.5)–5.5–7.0–(8.0) dm tall, with two to four leaves which are reduced upwards. Inflorescence a simple raceme with three to eight flowers; raceme interrupted by spathe-like, ensheathing bracts, bracts 1.1–2.8 cm long, reduced upwards, aristate tipped, 0.4–2.0 cm long. Bract ensheaths pedicel and a three-part bracteole, which is connate basally. Flowers perfect. Tepals linear to linear-lanceolate, free, three-nerved, persistent in fruit; tepals subequal, outer tepals slightly longer, 0.9–1.7 cm long, 2.0–4.0 mm wide; tepals whitish yellow centrally and dull green marginally on the inside, and dull yellowish white on the outside. Stamens nine, six in the outer cycle, three in the inner cycle, rarely totaling 10; filaments glabrous, dilated basally, divergent at anthesis, one-nerved, 4.2–5.2 mm long; anthers versatile, laterally dehiscent, 2.4–3.0 mm long. Gynoecium subdivided basally into three free stipitate carpels by an intercarpellary gland; lateral septal walls only appressed, unilocular along floral axis; styles short and free. Capsule erect, leathery, distinctly three-carpellate and dehiscence via septicidal separation; seeds numerous. Seeds reddish brown, glabrous, ellipsoidal with distal appendages; seeds 1.1–1.5 mm long, appendages 1.7–2.5 mm long. Flowering September to October; fruiting October to November. Locally abundant; pocosins, pine swamps and savannahs of the southeastern coastal plain. Chromosome number unknown.

SPECIMENS EXAMINED

FLORIDA: NW Florida, borders of swamps, September, A. H. Curtiss 15368 (MO); Near Argyle, bogs in pine barrens, 3 October 1901, A. H. Curtiss 6925 (MO).

NORTH CAROLINA: Brunswick Co., SW of Wilmington, wet meadow, 29 September 1931, *J. Bright 6271* (CM); WNW of Southport, flat sandy, peaty, rather damp pinelands, 4 April 1961, *H. H. and C. M. Iltis 17,220* (WIS); Pond pine savannah, 5.0 mi N of NC 211 and US 17, 20 October 1975, *S. Rich 83* (WIS); Sandy seepage area, E of NC 133, near entrance to Boiling Springs, 26 September 1966, *C. R. Bell 18,566* (WIS); New Hanover Co., Wilmington, *s.d.*, *Curtis s.n.* (ex herb. A. Gray) (MO); Onslow Co., Savanna on NC 172, NE of US 17 and NC 172, 12 September 1949, *A. E. Radford 5035* (WIS); Flat, wet pine savannah, SW of Holly Ridge along US 17, 13 October 1977, *F. H. Utech 77-513* (CM); Pender Co., Pine savannah, 4.0 mi NE of Hampstead on US 17, 14 October 1977, *F. H. Utech 77-515* (CM).

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FLORAL VASCULAR ANATOMY OF THE MONOTYPIC JAPANESE *METANARTHECIUM LUTEOVIRIDE* MAXIM. (LILIACEAE-MELANTHIOIDEAE)

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ABSTRACT

The Japanese endemic *Metanarthecium luteoviride* Maxim. is a perennial herb with a simple, rarely branched, elongate raceme, and has different tribal positions in the Englerian and Hutchinsonian subdivisions of the primitive liliaceous subfamily Melanthioideae. This study reports on the floral vascular anatomy of this Asian species and is directed at a re-examination of its tribal position. The single flower at each node is subtended by both a bract and a bracteole. The six-merous flower is perfect, though basally both perigyny and a floral tube occur. Incomplete fusion along the basal septa results in the formation of septal (nectiferous) glands. The versatile anthers are abaxially attached and dehisce via longitudinal, lateral slits. Rhaphides are common within the gynoeceum at all stages of development. The fruit is a loculicidal capsule, though in flower there are both septicidal and loculicidal subdivisions of the central placenta. The seeds are not appendaged.

Floral vascularization is derived from a six-bundled, axial vascular configuration within the pedicel. Because of perigyny, common fusion bundles are formed between the six axial bundles. The lowest and first formed of these common bundles are the three common outer tepal-outer stamen-dorsal bundles, whereas the upper three are the common inner tepal-inner stamen bundles. Above the perigynous zone, these six common bundles divide into their various components. The common tepal bundles of both cycles subdivide into a median and two laterals. The stamen bundles of both cycles are fusion products, though throughout much of the perigynous zone, the two elements of the fusion product are separated. The dorsals are also fusion products, though their origin occurred below the perigynous zone. The six axial bundles which formed the common

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bundles continue vertically and establish the ventral supply and three fusion septal axials. The vertical course of the latter is limited. There is no dorsal branching or interconnection between the dorsal and ventral supplies. The three dorsals terminate in the elongated style.

INTRODUCTION

The Japanese *Metanarthecium luteoviride* of Maximowicz (1867) is a primitive, perennial, scapose lily. "Nogi-ran," the most frequently used Japanese common name for this species, refers to a beard, that is an elongated Asian chin-beard. Another common name noted by Makino (1974, nr. 3318), but less frequently used, is "kitsuneo-o," which means the tail of a fox. Both common names are allusions to this species' elongated raceme of many, small, pale yellowish green flowers. The Latin specific name is also in reference to the yellowish green flowers. Furthermore, the leaves also have a yellowish green cast.

Metanarthecium luteoviride is endemic to the Japanese Islands (Ohwi, 1965a, 1965b; Kitamura et al., 1965; Makino, 1974; Numata, 1974), and occurs in open sunny sites southward from the northernmost island of Hokkaido, through the major islands of Honshu, Shikoku, and Kyushu. On Yakushima, a small volcanic island south of Kyushu, according to Kitamura et al. (1965:151-152) and Ohwi (1965a, 1965b), a dwarf variety with longer pedicels occurs, that is, var. *nutans* Masamune.

Additional variation southward has been reported from Taiwan (Formosa) (Hayata, 1911), and has been recognized as a second species, *Metanarthecium foliatum* Hayata. Whether the Japanese *M. luteoviride* and the Formosan *M. foliatum* are distinctive or conspecific is debatable, and certainly in need of further systematic research. Nevertheless, this genus with either one or two species is limited to the temperate islands on the western edge of the Pacific Ocean.

Metanarthecium luteoviride has been illustrated twice (Makino, 1974, nr. 3318; Kitamura et al., 1965:151-152, pl. 42). In both floras, the accompanying descriptions are in Japanese. The recent English version of Ohwi's *Flora of Japan* (1965a) does give a good morphological description of *Metanarthecium*, which significantly upgrades the previous western accounts of this species (Maximowicz, 1867; Baker, 1876; Bentham and Hooker, 1883; Engler, 1888; Krause, 1930).

Among the primitive groups of lilies, frequently treated as the subfamily Melanthioideae or as the segregated family Melanthaceae, the tribal position of *Metanarthecium* differs greatly between the Englerian (Engler, 1888; Krause, 1930), and the Hutchinsonian (Hutchinson, 1934, 1959) systems. The genera of the Englerian Helonieae include *Xerophyllum* Michx., *Chamaelirium* Willd., *Helonias* L., *Chionographis* Maxim., *Heloniopsis* A. Gray, *Ypsilandra* Franch., and

Metanarthecium Maxim. The only difference between Engler's (1888) and Krause's (1930) circumscription of the Helonieae is the latter's addition of the Himalayan genus *Ypsilandra*, which has affinities to *Helonias* and *Heloniopsis* (S. Kawano, personal communication). The genera grouped into Hutchinson's Narthecieae (1934, 1959), on the other hand, include *Pleea* Michx., *Tofieldia* Huds. (including *Triantha* Baker and *Japanolirion* Nakai), *Hewardia* Hook., *Xerophyllum* Michx., *Heloniopsis* A. Gray, *Clara* Kunth, *Narthecium* Huds., *Aletris* L. (including *Meta-aletris* Masamune), *Nietneria* Klotzsch, and *Metanarthecium* Maxim.

In Gates' review (1918) of the (Melanthioideae) Melanthaceae, a close relationship between *Metanarthecium* and *Narthecium* was stressed. However, the tribal position of *Metanarthecium* as well as its relationship to *Narthecium* (sensu Gates, 1918) remains unsettled.

A single, known chromosome count of $2N = 52$ by Satō (1952) has repeatedly been cited in the chromosome atlases (Darlington and Wylie, 1955; Fedorov, 1969; also Kitamura et al., 1965) for *Metanarthecium luteoviride*. With only a somatic number and incomplete karyotypic morphology, it is difficult to infer a genome relationship between *Metanarthecium* and the other primitive lilies. However, the $2N = 52$ number is high in comparison to those known for the other tribal members, either in the Helonieae (Engler, 1888; Krause, 1930) or the Narthecieae (Hutchinson, 1934, 1959), and it is extremely probable that a polyploid genome origin can be assigned to *Metanarthecium*.

This report is a serial continuation of the floral vascular anatomical studies on primitive members of the Liliaceae-Melanthioideae (Utech, 1978a—*Xerophyllum*; Utech, 1978b—*Helonias*; Utech, 1978c—*Pleea* (= *Tofieldia*); Utech and Kawano, 1978—*Heloniopsis*). The following observations on the floral vascular anatomy and floral morphology of *Metanarthecium luteoviride* will be presented and organized so as to be comparative to our previous reports.

MATERIALS AND METHODS

Flowering and fruiting inflorescences of *Metanarthecium luteoviride* were personally collected in Japan—Honshu: Toyama Prefecture, Tateyama Mountain Range, open meadow above Bijyodaira in the North Japanese Alps, elev. 2400 m, 24 July 1975. These floral materials were fixed in Farmer's solution (3 absolute ethanol:1 glacial acetic acid) for 12 h, and transferred into 70% ethanol for long-term storage. Standardized paraffin embedding and sectioning ($14\text{--}16\ \mu$) was followed by staining in safranin and methylene blue (Johansen, 1940; Sass, 1958). A total series of 12 flowers and fruits were serial prepared. As an additional check on these preparations, whole flowers and fruits were cleared and stained in a NaOH-1% fuchsin mixture (Fuchs, 1963; Utech and Kawano, 1975, 1976). The remaining fixed material and the prepared microslides are serving as the vouchers (CM). Herbarium specimens from the following institutions (Holmgren and Keuken, 1974) have been examined: MO, WIS, TNS, KYO, MAK, TI, and TUS.

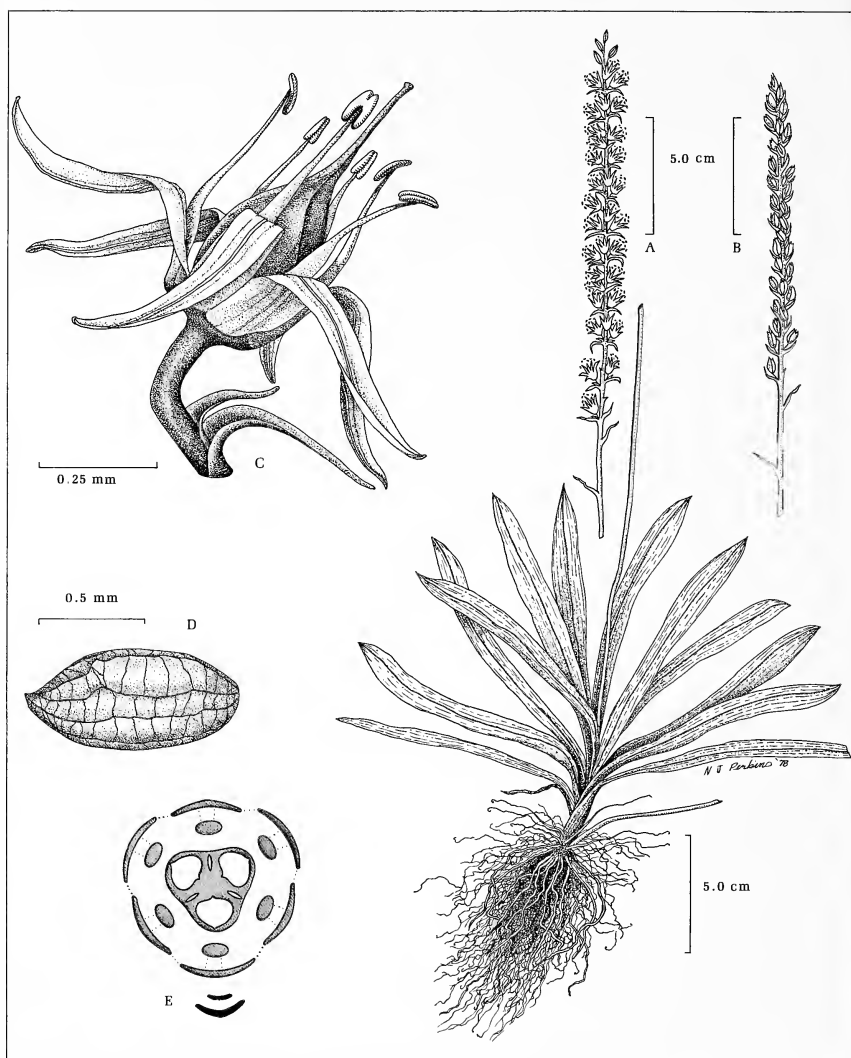


Fig. 1.—Illustration of *Metanartheceum luteoviride* Maxim., scale indicated. A) Flowering raceme with the upper and lower scape detached to show overall habit. B) Fruiting raceme, same scale as A. C) Enlarged flower showing the tepal-stamen arrangement, the abaxially attached, versatile anthers, the basal perigynous zone, and the short pedicel which is basally subtended by both a bract and a bracteole. D) A non-appendaged seed with several longitudinal striations and numerous cross striations shown. E) Floral diagram, bract and bracteole included. (drawing by Ms. Nancy J. Perkins)

OBSERVATIONS

Inflorescence, Bracts, and Bracteoles

Basally the scapes of *Metanarthecium luteoviride* are surrounded by a rosette of spreading radical leaves, which are yellowish green, glabrous, oblanceolate, gradually narrowed to their bases, and abruptly acuminate terminally (Fig. 1). The scapes are usually between 15 and 55 cm tall. The taller individuals of a population may be once or more rarely, twice branched from the lower floral nodes of the spike. The lower scape is weakly glandular-pilose, and interrupted by several, progressively smaller leaflike bracts.

The erect flowering spikes are usually between (5)–10–20 cm long, and this length is directly proportional to the number of flowers present (Fig. 1). At each node of the spike, the solitary flower is subtended both by a linear bract, which is longer than the pedicel, and by a shorter, linear bracteole. Both the bract and the bracteole, which basally subtend a given pedicel, depart in the same direction and from the same side of the spike axis (Fig. 1). Both bract and bracteole are green and vascularized.

Pedicel Morphology and Vascularization

The pedicels in *Metanarthecium luteoviride* are relatively short (2.0–4.0 mm) in comparison to the overall flower size. In cross-section, the pedicel is circular, and lacks the glandular-pilose epidermal modifications, which characterized the lower scape. Within the pedicel there are two vertically separated levels where bundle divisions and fusions occur. Basally in cross-section the lower pedicel has a ring of six central axial bundles (Figs. 5A, 6A). These bundles are large and distinct with normally arranged xylem and phloem. No sclerenchymatous sheath surrounds these bundles. Within the lower one-third of the pedicel, three fusion bundles are formed, each 120° apart, via side branches from each of the six ring bundles (Figs. 2, 5B, 6B). At progressively higher levels, these three fusion bundles will establish the outer tepal, outer stamen, and dorsal supplies (Figs. 5–8). Because these component traces depart at different horizontal levels, it is important to stress that these three bundles had a fusion origin at a lower pedicel level. Also, because of this lower fusion origin, reference to these main bundles up to their level of trace subdivision will be either as the common outer tepal-outer stamen-dorsal (OT-OS-D) bundles or the outer tepal-outer stamen (OT-OS) bundle (Figs. 5–8).

Within the upper one-third of the pedicel, there is a second series of radial divisions again involving the six axial bundles. However, this radial division with departing side branches occurs on the opposite side of the axial bundles as the lower and earlier divisions. Following

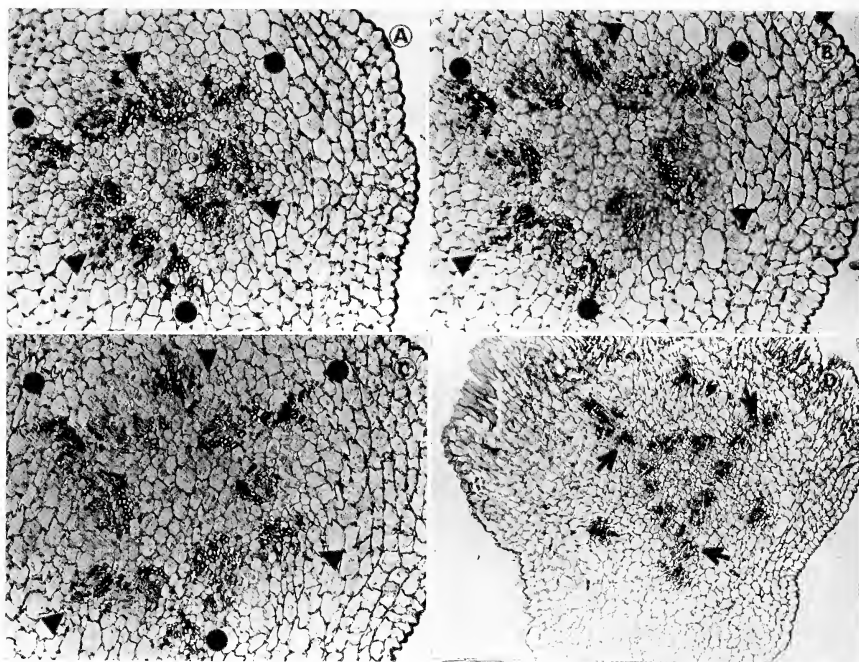


Fig. 2.—Serial cross-sections from the middle to upper pedicel in *Metanarthecium luteoviride*. A–C) Mid-pedicel, vascular transition from the nine- to the 12-bundled configuration. The three common OT-OS-D bundles formed at a lower pedicel level are marked by solid dots, whereas the three alternate radii along which the three common IT-IS bundles are formed and depart are marked by solid triangles. A ring of six axial bundles remains centrally in C (40 \times). D) Upper pedicel vascularization showing the formation of the three dorsals (arrows) from the common outer bundles, the departure of the three inner common bundles, the six axial central bundles, and the change from a circular to a six-lobed cross-section (30 \times).

fusion three new bundles are formed. Each is 120° apart and 60° from a common OT-OS-D bundle. The three new fusion bundles will establish at higher levels the inner tepal and the inner stamen vascular supplies (Figs. 5–8). The lower fusion bundles will be referred to as the common inner tepal-inner stamen (IT-IS) bundles up to their level of subdivision, which occurs above the level where the common OT-OS divides. The outer and inner common supply bundles have a similar pattern of origin. The common bundles are also an indication of the degree of perigyny present in *Metanarthecium luteoviride*.

Within the pedicel, the following changes in bundle configurations are observed (Figs. 5–8). Basally, there are six central axial bundles. In the lower one-third, there are nine bundles, that is, the six axial

bundles and the three new OT-OS-D common bundles. In the upper one-third region, there are 12 bundles, that is, the nine, which were continuous from below, and the three newly formed fusion bundles, that is, the IT-IS common bundles. The upper pedicel has 12 bundles, which are all on different radii. The three common OT-OS-D bundles are the closest to the periphery, whereas the IT-IS bundles are not as close to the periphery. The six axial bundles, on the other hand, remain in their same relative central position as in the pedicel base.

Receptacle Base, Perigynous Zone, and Floral Tube

The transition from the upper pedicel to the lower receptacle base is associated with a gradual increase in cross-sectional area (Figs. 5 B-D; 6 B-D). The dorsals (D) are formed in this expanding zone. From each of the common OT-OS-D bundles which are broadly trilobed at this level, a dorsal (D) is cut off adaxially from each of these compound bundles (Figs. 5 D-F; 6 D-F). Because these compound common bundles are in a peripheral position, the dorsals are freed peripherally. There is no indication of locule opening at this level, subsequently there is no net outward movement of the freed dorsals (D). Furthermore, because the dorsals (D) were derived from the common OT-OS-D bundles, which in turn were lower pedicel fusion products, the dorsals are indirect fusion products.

Broadening of the cross-sectional area of the receptacle base increases significantly following the formation of the dorsals. Whereas the pedicel was circular in cross-section, the receptacle base is broadly six lobed. Three of these lobes are larger than the other three. The outermost edges of the larger lobes are aligned along the radii of the triwedged OT-OS bundles. The three IT-IS bundles, on the other hand, are associated with radii that bisect the three smaller lobes (Figs. 5 D-F; 6 D-F).

The low level of locular opening in *Metanarthecium luteoviride* indicates perigyny. The three locules open before any tepal or stamen traces of either whorls are established, and below the levels where the tepals and stamens are cut off (Figs. 5 E-G; 6 E-G). There is total adnation in both flowering and fruiting material of the floral envelope to the gynoecium. Another indication of perigyny is that the gynoeceal vasculature is established before either the tepals and stamens are cut off or their vasculature established.

The perigynous zone extends vertically for some distance before the perianth and the adnate stamens are freed (Fig. 7). The first indications in cross-section of this separation are six crescent-shaped gaps (Figs. 5 F-G; 6 F-G). The ends of each gap are between the common outer and the common inner tepal-stamen supplies. The gynoecium is therefore not freed along either the dorsal or septal regions, but in between.

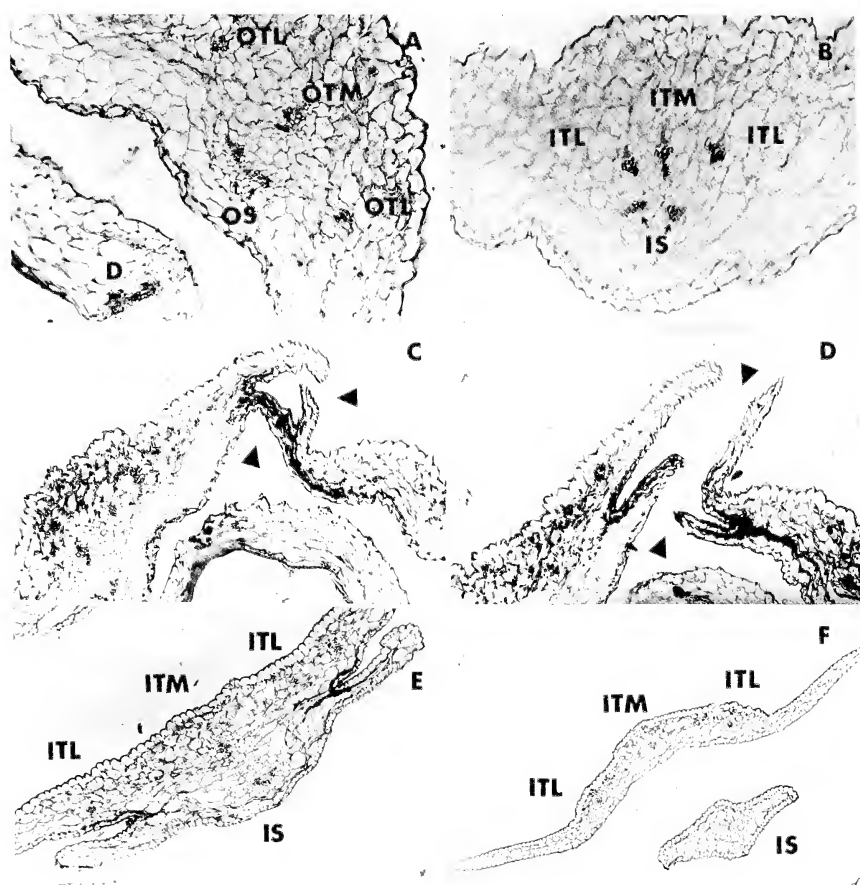


Fig. 3.—Serial cross-section showing tepal and stamen vascularization and adnation in *Metanarthecium luteoviride*. A) A carpellary dorsal (D), and an outer, five-bundled set within the floral tube are shown; the latter set is represented by two outer tepal laterals (OTL), an outer tepal median (OTM), and two inner bundles, which fuse to form the outer stamen (OS) bundle (60 \times). B) Floral tube, same height as A, but showing an inner, five-bundled set, that is, two inner tepal laterals (ITL), an inner tepal median (ITM), and two inner bundles which fuse to form the inner stamen (IS) bundle (60 \times). C) Fused margin of the floral tube between an outer and inner tepal (triangles) (60 \times). D) Section above C showing the marginal separation of the floral tube between an outer and inner tepal (triangles) (60 \times). E) Section above D showing inner stamen epitepaly; tepal and stamen bundles indicated (50 \times). F) Lower, non-recurved, inner tepal subtending basally a dilated inner filament (25 \times).

As these gaps enlarge and meet, a floral tube is formed, which surrounds the gynoecium (Figs. 5 F–G; 6 F–G). Stamen adnation (epitepaly) also characterizes this floral tube, because neither the outer nor the inner stamens or their traces are established when the floral tube is cut off. Neither the outer carpellary wall nor the inner wall of the floral tube, that is, the dilated adaxial filament surface, are characterized by any special type of epidermis, which could function as a basal nectary within the floral tube.

Within the floral tube, the subdivision of the common OT-OS bundle into three outer tepal traces and a double (bifid) outer stamen trace occurs before the subdivision of the common IT-IS bundle into the three inner tepal traces and a double (bifid) inner stamen trace. That all this trace formation from a compound bundle formed in the lower pedicel occurs within the floral tube and the perigynous zone attests to the degree of adnation and cohesion previously unreported for the genus *Metanarthecium*.

Tepal and Stamen Morphology and Vascularization

The freed portions of the six tepals are sublinear to lanceolate, 6.0–8.5 (–11.0) mm long and equal (Fig. 1). The successive separation of these six tepals and the six associated stamens from the floral tube is shown in Figs. 3, 5 F–J, and 6 F–J. During anthesis, the freed tepals of both cycles are recurved or spread (Fig. 1). Tepal color is localized, and similar within both cycles. On the outer surface of the six tepals, there is a central zone on both sides of the midrib, which is light green, whereas the outer marginal surfaces are a yellowish white. The tepals persist into the fruiting stages.

The stamens are shorter than the tepals (Fig. 1). The filaments are basally dilated, filiform terminally, and glabrous (Figs. 3; 5 H–J; 6 H–J; 7). The filaments of *Narthecium*, in comparison, are densely pubescent. In *Metanarthecium*, the filament and anther lengths of both cycles are equal. The observed outward divergence of the filaments during anthesis is associated with the simultaneous recurving of the tepals, which is directly due to the staminal epitepaly above the perigynous zone (Fig. 7).

The oblong anthers are attached to the attenuated filament tips slightly below the anther's mid-length point on their outer, abaxial surface. The anthers are subsequently versatile, and in conjunction with the divergent filaments a wide pollen dispersal zone is created at the same level as the capitate stigma. Anther dehiscence is via longitudinal, lateral slits. The endothelial cell walls of the anthers are marked by banded thickenings.

Because of the basal perigyny, the floral tube, and the stamineal epitepaly in *Metanarthecium* and the subsequent compound, common

bundles, tepal and stamen vascularization will be presented simultaneously. Within the upper pedicel, six compound fusion bundles are formed (Figs. 5 A-E; 6 A-E). Three of these are the OT-OS-D common bundles, and the other three are the IT-IS common bundles (Fig. 8). The three dorsals (D) are cut off from the outer common bundles at a low perigynous level. The remaining portions of these common bundles, that is, the OT-OS common bundles, become broadly trilobed following dorsal (D) departure. Subsequently, each trilobed bundle is radially subdivided into three free bundles (Figs. 5 D-G; 6 D-G; 8). The central bundle of each triplet becomes the outer tepal median (OTM), whereas the two lateral bundles each undergo an additional division. Following this division, there are three peripheral sets of five bundles. Each set is 120° apart.

These three sets of bundles, the most peripheral within the perigynous and floral tube zones, establish the complete outer tepal and stamen vasculature (Fig. 8). The outermost bundle of each set is the OTM with a radially derived pair on each side. This outermost bundle pair establishes the outer tepal laterals (OTL) (Figs. 3; 5 G-J; 6 G-J; 8). The inner bundles of the above pairs will at a higher level fuse and establish the outer stamen (OS) traces. The two inner bundles, which contribute to the OS trace, run parallel in a vertical direction prior to their fusion (Figs. 3; 5 F-K; 6 F-K; 8). This fusion occurs as the outer stamens are freed from the adnate tepals within the epitepaly zone. The filament of each outer stamen, therefore, has a single fusion trace (OS). Each outer freed tepal, on the other hand, has two laterals and a median, that is, an OTL plus an OTM plus an OTL (Figs. 3; 5 G-J; 6 G-J; 8). Past descriptions (Baker, 1876; Engler, 1888; Bentham and Hooker, 1883; Krause, 1930; Ohwi, 1965) have incorrectly noted that the tepals are one-nerved.

The origin of the inner tepal and inner stamen vasculature is similar to that of the outer tepals and outer stamens (Fig. 8). Moreover, the subdivision of the IT-IS common bundle parallels that of the OT-OS common bundle. However, the formation of the inner three five-bundled sets along the septal radii occurs at a higher level than subdivision of the three outer common OT-OS bundles. Each freed inner tepal, like an outer tepal, has three bundles, that is, an ITL plus an ITM plus an ITL. The origin of the IS bundle, which involves unfused parallel traces, is identical to that of the OS bundle. There is consequently a fusion inner stamen (IS) trace in each inner filament.

Gynoecial Morphology and Vascularization

The narrowly ovoid to conical gynoecium of *Metanarthecium luteoviride* has several noteworthy modifications. Raphides are common throughout the gynoecium at all stages of development. They are es-

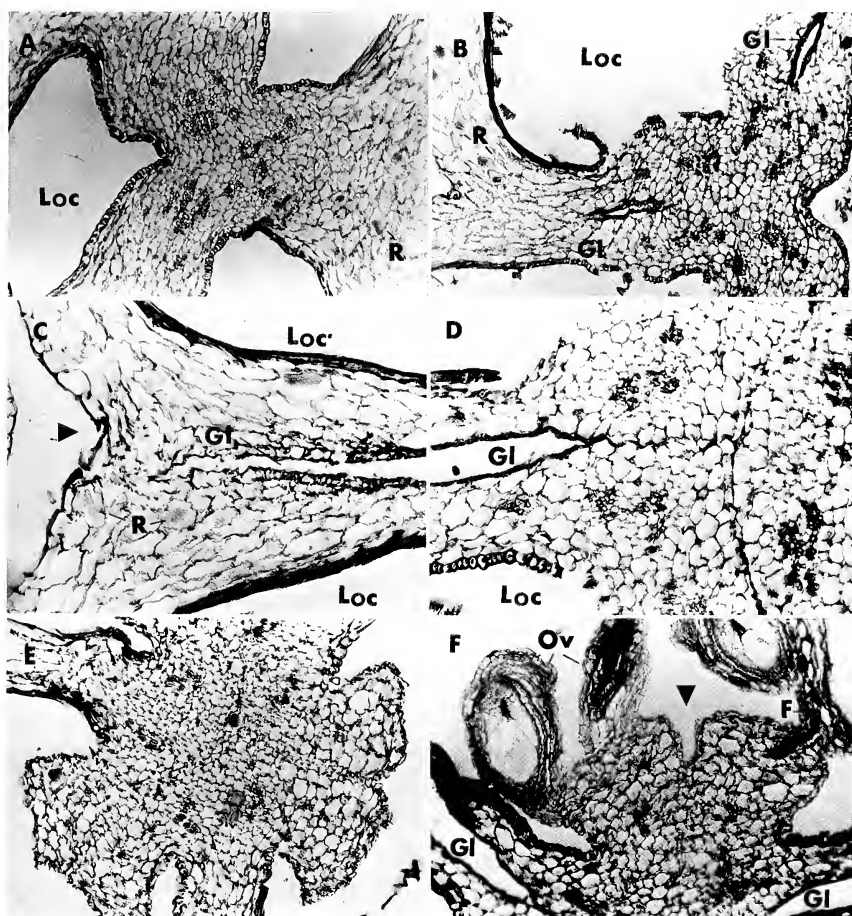


Fig. 4.—Serial cross-section of the gynoecium in *Metanarthecium luteoviride*. A) Gynoecial portion within the perigynous zone showing the wide septal wings and the central placenta, the subdivision of the axial bundles into the ventrals and the fusion formation of the septal axials (SA) (40 \times). B) Level of freed floral tube and gynoecium; section shows the inner formation of septal glands (Gl), the absence of septal axials (SA), and the subdivided ventrals; raphides (R) are common (40 \times). C) Enlarged section above B, showing the outer, radial extent of a septal gland (Gl), and its external opening (triangle); cells lining the gland (Gl) differ from those lining the locules (Loc) (60 \times). D) Section at the same level as C, but showing the inner, radial extent of a septal gland (Gl), and the septicidal subdivision of the central placenta; cells lining the gland (Gl) differ from those along the placental subdivision; ventrals present, but no funicular branching or ovular attachment occurs at this level (60 \times). E) Midgynoecial section showing loculicidal subdivision of the placenta (dotted lines); paired obturators extend into each locule; ventrals present (50 \times). F) Horizontal attachment of bitegmic ovules (ov) to obturators; funicular (F) traces derived horizontally from vertical ventrals; placenta loculicidally subdivided (triangle); septal glands (Gl) still present (50 \times).

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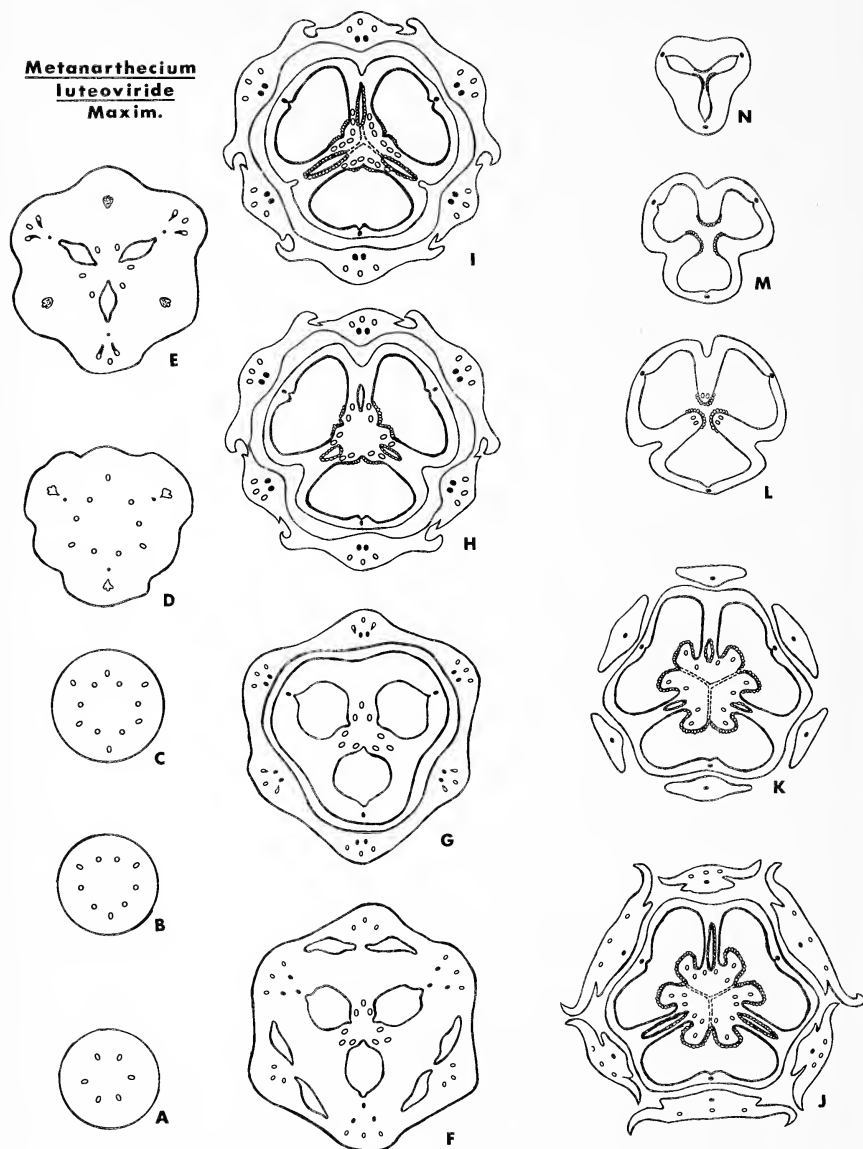


Fig. 5.—Serial cross-sections of *Metanarthecium luteoviride*. A) Lower pedicel with six-bundled configuration. B) Midpedicel with a nine-bundled configuration, the three additional bundles are the common outer tepal-outer stamen-dorsal bundles. C) Upper pedicel with a 12-bundled configuration, the three additional bundles are the common inner tepal-inner stamen bundles. D) Upper pedicel to receptacle transition, the three dorsals segregated from the outer common bundles. E) Perigyny at receptacle base, locules opening, outer common bundles subdividing into a median (OTM) and two lat-

pecially abundant in the septal wings and the funicular stalks. The three locules open via elongate slits along the dorsal radii within the lower perigynous zone. The gynoeceal vasculature is established at a lower level than that of the tepals and stamens.

The gynoeceum above the perigynous zone is surrounded by a floral tube (Figs. 5–7). Internal dorsal grooves run the whole gynoeceal length, external septal indentations are also present basally. The three septal (nectiferous) glands within the three septal wings open in the floral tube zone via the septal indentations (Fig. 7). Complete septicial subdivision of the central placenta occurs in the lower one-third of the gynoeceum. However, above this lower subdivision, the placenta is subdivided loculicidally. The upper one-third of this tricarpellate gynoeceum is therefore unilocular. The hollow, columnar style terminates in a shallowly trilobulate, capitate stigma. In fruit, both the style and the three carpels dehisce loculicidally, though in flower there are indications of both loculicidal and septicial dehiscence. In fruit, the carpellary walls are thin and chartaceous. The total seed number is approximately 24. The seeds are small (0.6–0.8 mm), reddish brown, oval, non-appendaged, and marked by several longitudinal striations, which are interrupted by numerous short transverse striations (Fig. 1).

1. *Septal Indentations and Septal Glands*.—As the floral tube is cut off and the gynoeceum freed, the septal wings are relatively thick in comparison to the outer carpellary walls. At this level, the central, massive placenta, is not subdivided loculicidally or septicially. However, within the locules there are carpellary grooves or notches (in cross-section) over the dorsals. These inner dorsal grooves extend up

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erals, inner common bundles near the periphery, six axials in three pairs near the center. F) Perigynous zone, the outer common bundles each represented by a set of five bundles, that is, the median (OTM), two tepal laterals (OTL) and two elements which will fuse to form the stamen bundle (OS), the inner common bundles subdividing into a median (ITM) and two laterals, septal axials (SA) formed between the paired axial bundles, gaps show zone of floral tube formation. G) Gynoeceum base freed from floral tube, both the outer and inner common bundles represented by five-bundled sets. H) Origin of the three septal glands, septal indentations also present, septal axials (SA) have terminated, the paired axials (ventrals) divided into several bundles, internal dorsal notch present, floral tube present. I) Septicial subdivision of the central placenta, septal glands with external connections into the floral tube, further subdivision among the vertical ventrals. J) Loculicidal subdivision of the central placenta, obturators present, septal glands present, marginal separation of the floral tube with tepals and stamens remaining adnate, the two elements of each stamen bundle fuse. K) Filaments freed from the tepals (not shown), septal glands and the loculicidal placenta division shown, obturators with stigmatoid papillae. L) Lower unilocular style, ventrals remaining, dorsal grooves shown. M) Mid-style, ventrals absent. N) Upper style transition to trilobulate, capitate stigma, dorsals present.

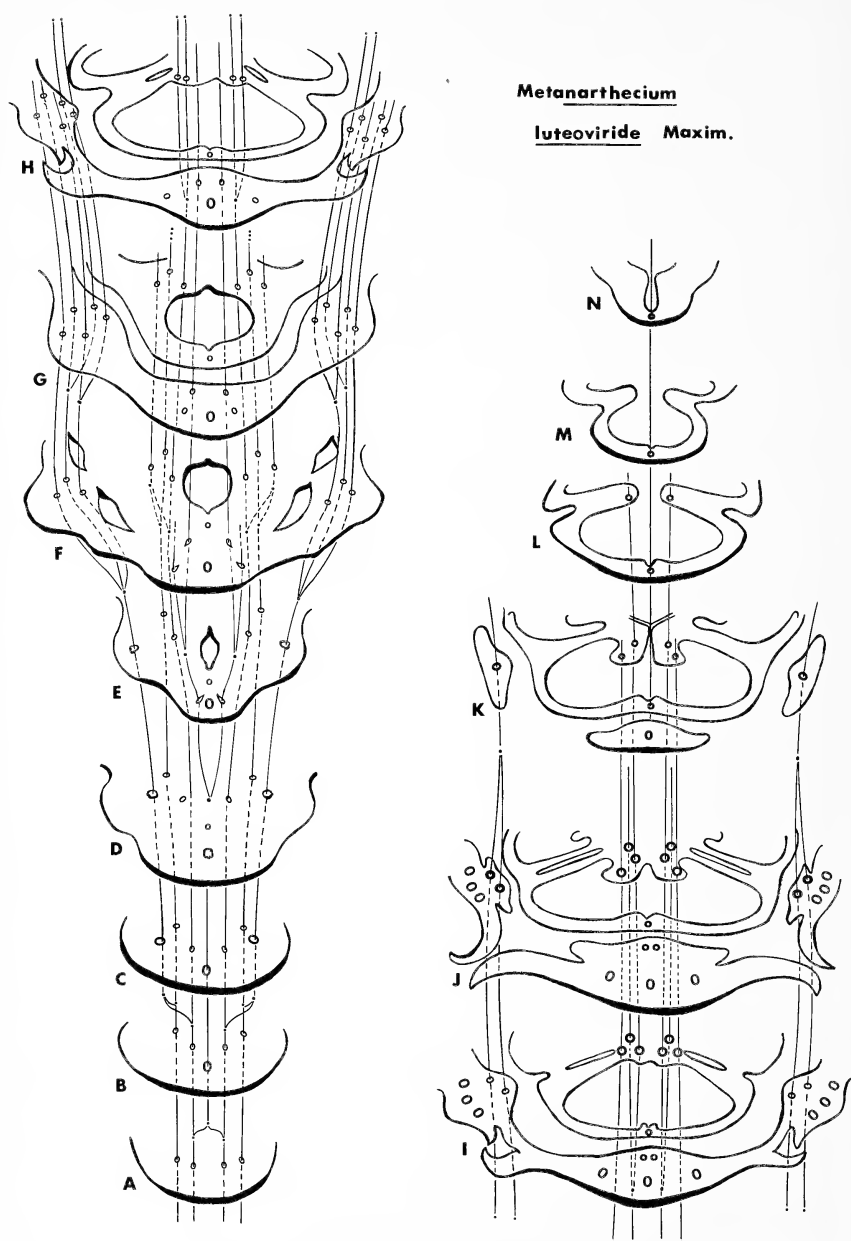


Fig. 6.—*Metanarthecium luteoviride*, cross-sections of Fig. 5 after transformational projections to give a semilongitudinal view, selected vascular bundles are connected, and the lettered cross-sections correspond to those in Fig. 5.

the whole inner gynoecial surface, as well as up the common style (Figs. 5 E–N; 6 E–N; 7). Usually such dorsal grooves are indicative of loculicidal dehiscence. However, there are also in the basal region external septal indentations (Figs. 5 H–I; 6 H–I; 7), which were formed as the inner stamen portions of the floral tubes were cut off. Normally such septal indentations are indicative of septicidal dehiscence. At a higher level within the floral tube, these outer septal indentations become openings for the septal (nectiferous) glands (Fig. 3 B–D). The epidermal linings of both the septal indentations and the outer carpelary walls are identical. The indentation cells do not stain differentially, and are not secretory. The three septal indentations are not observable in the mid- to upper gynoecium (Figs. 5 J–K; 6 J–K; 7).

The three septal (nectiferous) glands are formed in the lower periginous zone, but extend vertically for some distance within the septa (Figs. 4; 5 H–J; 6 H–J; 7). In cross-section, the three septal glands first appear as slits within the laterally fused septal wings. Confined to the three septal wings, the glands lack basally both external openings and central interconnections. Cells, which stain differently from those of the septal indentations, line the septal glands (Fig. 3 B–F). In all likelihood, these internal gland cells are secretory, and the three septal glands functioning as a basal, gynoecial nectary.

Two types of interconnections are observed within the septal glands. In cross-section, the radial length of the septal glands increases outward, and eventually opens into the three septal indentations along the periphery of the gynoecium (Figs. 4 C; 5 H–J; 6 H–J; 7). Although this gland opening level is basal, it is within the floral tube zone. Furthermore, with this opening the three carpels are only fused centrally within the central placenta. There are no indications of the three peripheral septal indentations above the gland opening level, because the outer margins of the septal wings are fused.

Following the opening of the septal glands and the closure of the outer septal wings, a second type of intragland connection occurs. It is internal, and completely subdivides the central placenta (Figs. 4 E; 5 I–J; 6 I–J; 7). The cells lining this intragland subdivision are similar to those of the surrounding placenta, that is, nonsecretory. The duration of this intragland connection and placental subdivision is vertically limited (Fig. 7). The septal glands, on the other hand, with their secretory cells extend vertically into the upper septal region of the gynoecium (Figs. 4 D–E; 5 H–J; 7).

The septal indentations, the septal glands, and the lower septicidal subdivision of the central placenta are strong indications of how incompletely the three carpels are fused. These septal modifications in conjunction with the floral tube function as a pollination-related nectary. The geometric configuration of the elongated style with its cap-

itate stigma and the versatile anthers is also related to this pollination system.

In the upper one-third of the gynoecium, there is complete loculicidal subdivision of the central placenta (Figs. 4 F; 5 J-K; 7). The upper gynoecium is therefore unilocular, and the columnar style is hollow. It is most interesting that while there are carpellary indications of both loculicidal and septicidal dehiscence, the fruit is a loculicidal capsule. This duality in gynoecial subdivision coupled to the septal (nectiferous) gland has not previously been reported for *Metanarthecium*.

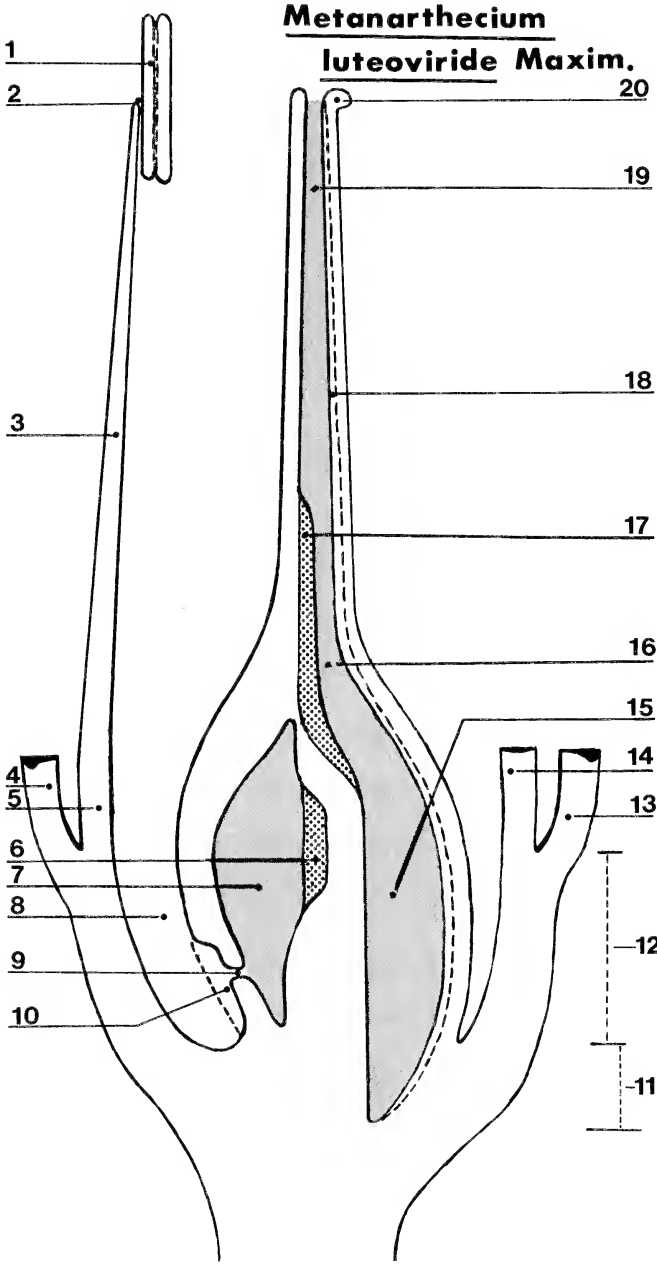
2. *Gynoecial Vascularization*.—The gynoecial vascular supply, like the locular opening, is established in the lower perigynous zone (Figs. 4 A; 5 E-F; 6 E-F; 7). The three dorsals (D), which represent indirect fusion products, are established within the perigynous zone from the three outer OT-OS-D bundles (Figs. 5 D-F; 6 D-F; 8). The complete ventral supply, on the other hand, is more complex than the dorsal supply. As the locules open, the ventral supply is established basally, in part, from the central six ring bundles. These bundles are coaxial with the six pedicel ring bundles (Fig. 8). The three dorsals (D), and the six bundles, which establish the ventral supply, have normally arranged xylem and phloem at this basal level.

The three dorsals (D) neither branch nor fuse with any of the ventral supply elements. Furthermore, the dorsals have an uninterrupted course from their perigynous level of formation to the capitate stigma tip (Fig. 8). A normal relationship between the xylem and phloem is maintained throughout the dorsal course. Because each carpel has an inner dorsal groove, which is the zone of loculicidal dehiscence, the dorsal bundles themselves are split as the capsule opens.

Ventral vascularization occurs at a low level due to the depression of the locules. As the three locules open, three septal zones and a large central placenta are established. The term septal zone is used, because perigyny occurs at this level (Figs. 5 E-F; 6 E-F; 7; 8). In each of the

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Fig. 7.—Median longitudinal diagram of a *Metanarthecium luteoviride* flower. Section passes through both a locule and a septum along the OTM-OS-D-IS-ITM diameter. Reconstructed in part from Figs. 5–6. Number code: 1) Versatile anther with a lateral, longitudinal dehiscence slit. 2) Abaxial anther attachment. 3) Glabrous inner filament. 4) Freed inner tepal (in part). 5) Freed inner filament. 6) Septicidal subdivision of central placenta. 7) Septal (nectiferous) gland. 8) Nectar space between the floral tube and the septal wall of the gynoecium. 9) External septal gland opening. 10) Septal indentation. 11) Height of perigynous zone. 12) Height of the floral tube and epitepaly zone. 13) Freed outer tepal (in part). 14) Freed outer stamen (in part). 15) Locule. 16) Unilocular upper gynoecium. 17) Loculicidal subdivision of the central placenta. 18) Inner dorsal groove. 19) Hollow styler canal. 20) Trilobulate, capitate stigma. Scale indicated.



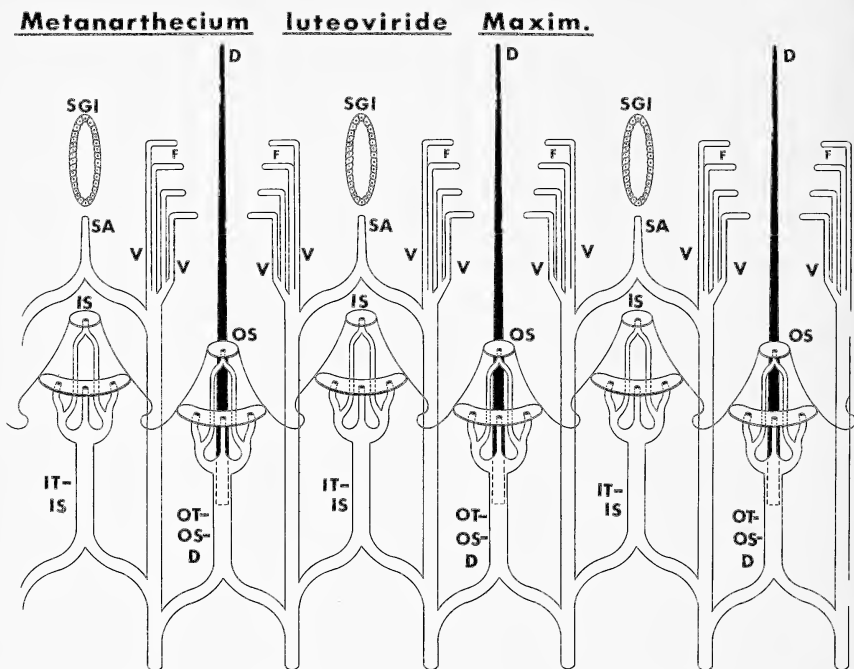


Fig. 8.—Summary longitudinal, roll-out diagram for *Metanarthecium luteoviride*. The following codes have been used for the various bundles: OTM = outer tepal median; OTL = outer tepal lateral; OS = outer stamen; D = dorsal; ITM = inner tepal median; ITL = inner tepal lateral; IS = inner stamen; OT-OS-D = common outer tepal-outer stamen-dorsal; OT-OS = common outer tepal-outer stamen; IT-IS = common inner tepal-inner stamen; V = ventral; F = funicular; SA = septal axial (fusion). Wavy line connecting the tepals and the stamens of both cycles represents the upper extent of the floral tube.

three septal zones, there is a pair of bundles. These six bundles, the three zonal pairs, are near the boundary between each respective bundle pairs' inner septal zone and the central placenta. All six bundles have normally disposed conducting elements.

A fusion bundle with normally arranged xylem and phloem is formed between each septal bundle pair via fusing side branches from this pair. These three bundles are the fusion septal axials (SA) (Figs. 4 A; 5 D-E; 6 D-F; 8). They extend for a very limited vertical distance, and abruptly terminate. Their origin and termination are within the septal perigynous zone. Moreover, the termination of the septal axials (SA) is within the same vertical septal plane, and slightly below the level where the septal (nectiferous) glands occur (Figs. 4; 5 D-I; 6 D-J; 7; 8). In fact, one replaces the other, that is, as the septal axials terminate within the vertical septal planes, the septal glands appear.

As the three septal axials end within the septa, the laterally located ventral pair bundles of each septa undergo both a series of subdivisions and inturnings. Each ventral pair bundle undergoes three or four successive radial subdivisions. The resulting division products are inturned or rotated such that their xylem elements oppose the dorsal (D) which is across their shared locule.

Also at this level, both the septal glands, and the septicidal subdivision of the central placenta occur. The septal, inturned bundles, which can number 24, that is, four per septal side or eight per locule, follow a vertical course at this level. Each isolated bundle functions directly as a ventral (V) bundle (Fig. 8). In cross-section, these bundles are arranged in an arc around the inner surfaces of the locules. A given locule, consequently has supplying ventral (V) bundles, which were derived from adjacent axial bundles of different septal zonal pairs (Fig. 8).

The ventral supply in *Metanarthecium* is not of the type where a single ventral bundle ascends vertically parallel to the floral axis and horizontal funicular traces are derived from it. Rather, numerous ventral bundles are basally segregated, and each has a parallel vertical course. There is also a one to one correspondence between these vertical ventrals (V) and their associated horizontal funicular (F) traces (Fig. 8). Ovule attachment and funicular trace (F) departure in *Metanarthecium* occurs after the central placenta is subdivided loculicidally. No ovule supply occurs when the central placenta is septicidally subdivided.

3. *Inner Gynoeceal Surface*.—The inner locular surfaces are lined by rather elongate, non-papilloid cells. These cells are replaced by a second, rather cubical cell type along the placental axes of the locules below the level where the placenta is subdivided loculicidally. This loculicidal subdivision of the central placenta occurs above the septicidal placenta subdivision. Whereas the ventral (V) bundle rotation is associated with septicidal placental subdivision, obturator formation and ovule attachment via locular inturning of the freed septal wing tips, are associated with the loculicidal placental subdivision. The obturator surfaces are lined with cells of the second type. Portions of the horizontal funicular stalks which are extensions of the obturators also have these cells. These cells are also present within the hollow style along the three septal sutures, as well as over the top of the capitate stigma. Because this cellular distribution corresponds to the pathway of pollen tube growth, a continuous stigmatoid support system is present.

SUMMARY AND CONCLUDING REMARKS

The most salient features of the floral vascular anatomy of *Metanarthecium luteoviride* include the following. The paired bract and

bracteole, which subtend each solitary flower, are vascularized. A six-bundled, axial configuration characterizes the lower pedicel's vasculature. No sclerenchymatous sheath occurs between the undifferentiated pith and cortex of the pedicel. The basal perigyny, which extends into a shallow floral tube, obscures the true locular depth and receptacle base.

Because of this perigyny, common fusion bundles are prevalent. Six such bundles are formed in the upper pedicel; one common bundle between each of the six axial bundles. The lowest formed common bundles are the three outer tepal-outer stamen-dorsal bundles. Slightly higher, the other three, the three common inner tepal-inner stamen bundles are formed. Within and above the perigynous zone, these six common bundles divide into their various component bundles.

The common tepal bundles, that is, the common OT and the common IT, subdivide into a median and two laterals. Each outer tepal has an OTL plus an OTM plus an OTL, and each inner tepal has an ITL plus an ITM plus an ITL. The three traces of each tepal are established within the upper perigynous zone. The stamen bundles of both cycles, that is, the OS and IS bundles, are fusion products. The two components of each fusion stamen bundles are derived from the same bundles which established the tepal laterals. Throughout much of the perigynous zone, the two stamen trace components are separated and only fuse as the stamens are cut off from the tepals. The dorsals are also fusion products. Though their origin occurs below the perigynous zone, the dorsals are from the same common bundles which supplied the outer stamens and outer tepals. There is no branching of the dorsals, and each terminated in the upper style.

The six axial bundles, which formed the common bundles, continue vertically up into the base of the perigynous zone, and establish the ventral supply and the three fusion septal axials (SA). The vertical course of the septal axials is limited, and they terminate below the septal (nectiferous) glands. The ventral supply consists of several, basally subdivided bundles per septum. Each bundle has a vertical course and a one to one correspondence with a funicular trace. There is no interconnection above the pedicel-receptacle transition zone between the dorsal and ventral supplies.

The gynoecium has several noteworthy features. There is incomplete fusion along the outer, basal septal margins, which results in the formation of three septal (nectiferous) glands. These septal glands each have an external opening into the floral tube. Raphides are common within the gynoecium at all stages of development. The fruit is a loculicidal capsule, though in flower there are both septicidal and loculicidal subdivisions of the central placenta. Furthermore, there are no interconnections between the septal glands and the zones freed by the

septicidal and loculicidal subdivisions. Though the seeds are not appendaged, they have several longitudinal striations, which are interrupted by numerous cross striations.

Under the Englerian system (Engler, 1888; Krause, 1930), *Metanarthecium* is placed in the tribe Helonieae, whereas Hutchinson (1934, 1959) places *Metanarthecium* in a larger and somewhat differently circumscribed tribe, the Narthecieae. Two genera, *Xerophyllum* and *Heloniopsis* (but not *Helonias*), are common to both tribes. There are some generic groupings within both tribes that are justified and others that are not. *Tofieldia* and *Pleea* are congeneric (Utech, 1978c). *Pleea tenuifolia* was transferred to *Tofieldia* on the basis of the floral vascular anatomy and morphology of the two (Utech, 1978c). The Japanese endemic *Japanolirion osense* Nakai has affinities to *Tofieldia*, and the floral vascular anatomy of the former should be examined. Hutchinson's separation of *Helonias* and *Heloniopsis* does not appear justified, because both share a large number of floral vascular and floral morphological characters (Utech, 1978b; Utech and Kawano, 1978). *Ypsilandra*, an Himalayan genus, has affinities to both *Helonias* and *Heloniopsis*, and also needs to be examined.

Metanarthecium does exhibit several characters in common with *Narthecium* (Utech, 1978c), *Xerophyllum* (Utech, 1978a), *Helonias* (Utech, 1978b), and *Heloniopsis* (Utech and Kawano, 1978), but there are some significant differences. These genera share a loculicidal dehiscence, an axial pedicel vascular configuration from which fusion bundles are derived, and a massive basal placenta, but differ in that *Metanarthecium* exhibits perigyny and septal glands and has non-appendaged seeds. *Tofieldia*, including *Pleea*, is completely different from the above group (Utech, 1978c). This report on the floral vascular anatomy and morphology of *Metanarthecium* must remain incomplete as far as an exact tribal evaluation is concerned, until additional genera from both tribes are examined.

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TWO NEW CARIBBEAN SUBSPECIES OF BARN OWL (*TYTO ALBA*), WITH REMARKS ON VARIATION IN OTHER POPULATIONS

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ABSTRACT

The Barn Owl (*Tyto alba*) population of the Isle of Pines, previously considered identical to *T. a. furcata* of mainland Cuba, is described as new; it is smaller than *furcata* and whiter than all but a few extreme specimens of that race. The population of the Bay Islands of Honduras, previously placed with *T. a. pratincola*, is also described as new; it is smaller and whiter than *pratincola*. A female of this new race was in heavy molt while feeding young. Sexual dichromatism is marked in many races of this species, so color comparisons must be made sex for sex. The characters and geographic range of *T. a. guatemalae* need to be reassessed.

INTRODUCTION

Only three specimens of the Barn Owl (*Tyto alba*) are known to have been collected on the Bay Islands, off the Caribbean coast of Honduras (Monroe, 1968:153). The first of these was taken by James Bond on "Bonacca Island" (=Isla Guanaja) on 29 February 1936, and is in the collection of the Academy of Natural Sciences, Philadelphia (ANSP). Bond (1936) assigned this specimen to the North American race *T. a. pratincola* (Bonaparte), which he stated "is known to range

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south to eastern Nicaragua." This statement was probably based on Ridgway (1914:607), who assigned a single Nicaragua winter specimen to this race. The other two Bay Islands birds were taken by A. C. Twomey at French Harbor, Isla Roatán, on 7 April 1947, and are in Carnegie Museum of Natural History (CM), where they were examined by Phillips in October 1977. He was struck by their small size when compared with specimens of *pratincola* from the United States, and noted some color characters as well. Parkes then borrowed Bond's specimen from the ANSP and continued the study.

One of the color characters noted by Phillips was the whiteness of the rectrices and secondaries of the Bay Islands birds. These are characters of the Cuban subspecies *T. a. furcata* (Temminck), so Parkes compared the three Bay Islands birds with a series of supposed *furcata* in CM. These included specimens from both mainland Cuba and the Isle of Pines. Quite unexpectedly, the birds from the latter locality proved to represent a distinctive population, as did the Bay Islands birds. Both populations are separable as subspecies.

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COLOR VARIATION

During the course of this study it became obvious that various authors have underestimated the amount and the consistency of sexual dichromatism in at least some forms of this species. Ridgway (1914:605) stated that the sexes of *T. a. pratincola* were alike in color, but added in a footnote: "Apparently, however, females *average* darker than males; that is to say, in the extensive series examined there are more females than males among the darker colored specimens and more males than females among those with pure white underparts." His description was divided into three sections—average plumage, dark extreme, and light extreme. Descriptions of the North American race in some state and regional works we sampled all mention color variation, and some go so far as to designate dark and light "phases" (Roberts, 1932:604). All state or imply that the sexes are alike in color, with the exception of Oberholser (1974:443). This author described an "ochraceous phase" and a "light phase" for males of *T. a. pratincola*, and stated of females: "Similar to corresponding phase of . . . adult male but averaging darker." Oberholser appears to be the only author to have noticed sexual dichromatism in the bills of Barn Owls. He

described the bills of male *pratincola* as "dull pearly white to vinaceous pink," with the cere "pale brown." The bill of females was described as "vinaceous buff, becoming white at tip; cere vinaceous buff." It is not clear whether these colors were meant to apply to living birds or to study skins. In any case, the difference Oberholser described is visible in most study skins of *pratincola*. The bills of males are usually of a clear, pale, uniform color, whereas those of females have dark sides and a noticeably paler tip, the pale color sometimes extending along the ridge of the culmen. This character can be useful in deducing the sex of unsexed or dubiously sexed specimens, but must be used with caution. Specimens in CM suggest that young males of *pratincola* have bicolored bills like those of adult females. And, of course, the bills of some study skins are so discolored as to be completely untrustworthy. The sexual difference is less obvious in the pale Caribbean populations discussed later in the present paper.

Among the New World (North and Middle America, Greater Antilles) specimens examined during this study, the sexes from any given area segregated out almost completely by plumage color. Virtually all males are paler than females. The most conspicuous color character is usually that of the underparts. Among 22 reliably sexed specimens in the CM series of *T. a. pratincola*, there are no males with the rich ochraceous-buff underparts described by Ridgway as the "dark extreme," nor are there any females of the "light extreme" with pure white (but more or less speckled) underparts. Females appear to be more variable than males, in that some females have paler underparts, white washed with some shade of buff. Males generally have pure white underparts (more or less speckled), but some have a very light wash of buff over some areas. There is some evidence that juvenile males may regularly have a buffy stain on the breast (sometimes just the sides of the breast), but we have examined no specimens that illustrated molt from a buffy to a whiter plumage, which would help to confirm this as a character of juveniles. In any case, in the CM series there is no overlap between males and females of *T. a. pratincola* in color. A few specimens seen in other museums indicate that color segregation is not absolute. ANSP 86424, for example, a specimen from Vermillion Parish, Louisiana, is labelled as male, has the small measurements of that sex, but is a "dark phase" bird (although by no means of the dark extreme of *pratincola*).

Among the other populations studied for this paper, the generalization about sexual dichromatism in underparts color applies, but must be modified in accordance with the general darkness or paleness of the taxon. Dickey and van Rossem (1938:225) stated that four females of *T. a. guatemalae* (Ridgway) from El Salvador were "both collectively

and individually darker throughout" than seven males. Often overlooked are variations in pigmentation in areas other than the underparts. Especially important are the markings of the remiges and rectrices; again, in all series studied for this paper, females inevitably have such markings darker and/or more extensive than do males. Ridgway's reluctance to make a more definite association between color and sex may well be due to missexed specimens in the older component of the USNM collection. The series we have examined indicate that if the sexes of these subspecies of Barn Owl are not wholly separable by color alone, exceptions are decidedly rare. The principal point to be made here is that among the populations of North and Middle America and the Antilles, color comparisons *must* be made sex for sex when attempting to assess geographic variation.

In the species as a whole, the amount of sexual dichromatism varies geographically. Witherby (*in* Witherby et al., 1938:345) listed a number of color characters differentiating the sexes of the nominate race *T. a. alba* (Scopoli) of Europe, all involving increased pigmentation of females. Of the darker European race *T. a. guttata* (Brehm), however, Witherby (*in* Witherby et al., 1938:347) wrote: "ADULT FEMALE.—Like male and not differing as female does in *T. a. alba*." Mees (1964:5) stated: "There do not seem to be any differences in plumage between males and females in the species of Striges dealt with here," which included the Australian race *T. a. delicatula* (Gould). Parkes confirmed this statement, finding no apparent sexual dimorphism in any color character in the 31 sexed specimens of *delicatula* in the AMNH. On the other hand, the AMNH has 44 sexed specimens of the widely distributed South Pacific race *T. a. lulu* (Peale), of which Parkes was able to predict correctly the sex of all but one male and one female on the basis of underparts color alone.

SIZE VARIATION

Authors are in general agreement that male Barn Owls are smaller than females. Measurements made for the present study confirm this, but the *amount* of size dimorphism has been difficult to determine. The series of the insular populations are relatively small, and often skewed as to sex representation. The measurements of Ridgway (1914) are not directly comparable with ours, as they were made differently, but the relationship between the measurements of the sexes should be similar. The following figures indicate the percentages by which our mean measurements of females of *pratincola* exceed those of males, with the similar percentage computed from Ridgway's figures in parentheses: wing 2.3% (2.5%); tail 5.0% (2.2%); bill 3.0% (2.3%); tarsus 2.9% (−3.3%). Some of these differences (such as that in the tarsal measurements) may be attributable to missexed specimens in the

USNM, but also possibly to the geographic origin of Ridgway's series, which included a high proportion of specimens from California and Mexico. Specimens from California that we have measured (see Table 1) and Ridgway's table (1914:606) indicate that these and Mexican birds are appreciably smaller than those from most of the United States. As the type locality of *pratincola* is in Pennsylvania, we have felt justified in excluding these Pacific Coast and Mexican specimens when characterizing the subspecies *pratincola*. Ridgway himself, although not mentioning these size differences, pointed out that Pacific Coast specimens in general differ in color from others assigned to *pratincola*, and might ultimately prove separable. This question is outside the scope of the present paper, in which all references to *pratincola*, unless otherwise specified, may be assumed to apply to the populations of the United States other than the Pacific states.

The determination that a specimen has been missexed must of course be made cautiously, to avoid circularity of reasoning. The dimorphism in color and in size in the populations considered here is sufficiently consistent so that we are suspicious of the occasional very large and dark specimen sexed as male, or pale and small sexed as female, unless the sexing has been well documented by label notes on gonad condition; few of the specimens examined had any such documentation.

For this paper the wing was measured flattened on the rule, to attain the maximum measurement. Remiges and rectrices obviously worn more than 1 mm were excluded. The tails of these populations are variably forked, both geographically and individually. The normal tail measurement, which is a diagonal from the base of the central rectrices to the tip of the longest (in this instance outermost), was found to be difficult to take consistently, with the variation in tail spreading effected by the preparator complicating the natural variation. Far more consistent measurements were made by measuring the length of the central rectrix, a straight (not diagonal) measurement, so this somewhat unorthodox technique has been used for this paper.

SYSTEMATIC ACCOUNTS

Tyto alba niveicauda, new subspecies

Holotype.—CM 39,991, male (presumably adult) from Los Indios, Isle of Pines, Cuba, collected by G. A. Link, Sr., on 20 January 1913 (field number 535).

Characters.—Nearest *furcata* of mainland Cuba, but tail shorter and wing averaging shorter (see Table 1). Sex for sex, averaging whiter and paler than *furcata*; of 18 Cuban males, only four matched a series of five from the Isle of Pines in this respect. The few Jamaican specimens of *furcata* seen suggest that there might be slightly more overlap in color with *niveicauda* than is true of topotypical Cuban *furcata*. Comparisons here

Table 1.—Measurements in millimeters of adult Barn Owls (see text for methods of measuring).

Sex	Flattened wing	Central rectrix
	Observed range (Mean) \pm SD (N)	Observed range (Mean) \pm SD (N)
<i>Tyto alba pratincola</i> (U.S. except Pacific states)		
Males	322–357 (341.3) \pm 7.87 (13)	125–138 (130.5) \pm 4.55 (14)
Females	335–357 (347.8) \pm 7.11 (13)	131–144 (136.0) \pm 3.88 (15)
<i>Tyto alba pratincola</i> (California and one Oregon)		
Males	322–339 (331.2) \pm 5.05 (10)	120–135 (127.0) \pm 4.78 (10)
Females	334–348 (340.0) \pm 4.20 (11)	127.5–142 (134.4) \pm 4.51 (11)
<i>Tyto alba furcata</i> (Cuba)		
Males	332–349 (341.8) \pm 4.94 (9)	128–138 (133.8) \pm 3.52 (12)
Females	345–359 (353.8) \pm 4.50 (4)	134–141 (138.0) \pm 2.38 (7)
<i>Tyto alba furcata</i> (Jamaica)		
Males	332, 333	126, 133
Female	345	136
<i>Tyto alba niveicauda</i>		
Males	318–338 (330.8) \pm 7.66 (5)	122.5–128 (126.4) \pm 3.60 (5)
Female	347	128
<i>Tyto alba bondi</i>		
Male	301	114
Females	296+ (very worn), 316	114, 114.5

are made between *niveicauda* and the majority of *furcata* specimens. *Males*—gray marbling of upperparts coarser so that more white background shows, giving a paler appearance. Rectrices completely white, with no markings whatsoever. Primaries paler, with dark spots along the shaft reduced, especially on proximal primaries; in extreme instances (CM 41,383), these marks reduced to a single spot on the four outer primaries only; buffy wash and fuscous freckling of tips of inner primaries reduced or lacking, with the palest birds (CM 36,064; 41,383) having the inner primaries unmarked white. All but innermost secondaries (=tertials) pure white, with at most a small linear dark mark midway along shaft, and slight fuscous freckling on outer web near tip of the three or four secondaries immediately distal to tertials; all specimens have at least some secondaries pristinely white. In most *furcata*, all secondaries have at least two spots along the shaft, and have their outer webs freckled against a pale buff background, from all to about the distal half of their length. Pigmentation of the small feathers of the lower half of the facial disk of *niveicauda* reduced or lacking. Tiny fuscous dots on white underparts averaging fewer, sometimes nearly lacking.

Females—the one available female of *niveicauda* is more lightly marked than any examined female of *furcata*. Gray marbling of upperparts paler. Dark rectrix spots reduced to linear marks along the shaft on the inner three to four pairs; the only trace of buff is a stain around the dark spots of the central pair of rectrices only, and freckling is confined to the tips of the two central pairs. The two outermost pairs of rectrices are

pure white. In most *furcata* the rectrices have two to four conspicuous dark spots (full crossbars in darker specimens), diminishing in size from inner to outer rectrices; the central pair is more or less washed with buff, diminishing outwardly so that little or none remains on outermost pair; some fuscous freckling at tips of all rectrices in darker and all but two outer pairs in paler specimens. In even the palest extreme "females" of *furcata*, only the outermost pair of rectrices were pure white (versus two outermost pairs in *niveicauda*), and measurements suggest that three out of five such pale *furcata* "females" were missexed males. The primaries of *niveicauda* are much paler than in most *furcata*, with dark crossbars reduced in size and number; inner primaries with outer margins white (buff in most *furcata*), with freckling much reduced. Outer and inner secondaries pure white except for small shaft-spots and some freckling on outer web; a few central secondaries pure white. Very few specimens of *furcata* have any pure white secondaries, and some of these (as indicated above) may be missexed males. Pigmentation of facial disk and ventral spotting reduced as in males. Cinnamomeous or buffy wash of white underparts much reduced, confined to sides of breast, as in palest extreme examples of *furcata*.

Range.—Known only from the Isle of Pines (Isla de Pinos), south of the western end of Cuba, Greater Antilles.

Remarks.—Todd (1916:235–236) discussed the CM series of Barn Owls from the Isle of Pines. He mentioned the fact that only one specimen exhibited any markings at all on the rectrices, but overlooked the significant fact that this was the only female in the series. The Isle of Pines, although separated from Cuba by a relatively narrow channel and presumably relatively recently disconnected from Cuba (Bond, 1956:78), is a moderate center of differentiation for birds. There are about eight valid subspecies of birds endemic to the island, including the Barn Owl described here. A few bird species vary geographically on Cuba itself. In four of these (*Gymnoglaux lawrencii*, *Mimocichla plumbea*, *Vireo gundlachi*, *Quiscalus niger*) the subspecies of western Cuba is shared with the Isle of Pines (Garrido and Garcia Montaña, 1975). In *Tyto alba*, however, the white extremes of *furcata* were collected all over Cuba and were not concentrated in the west, nor do these individuals come any closer than darker birds to the measurements of *niveicauda*.

Inclusion of the North American *T. a. pratincola* as an accidental visitant to Cuba (Garrido and Garcia Montaña, 1975:70) rested until recently on the willingness of Bond (1964:6) to accept as valid the alleged Cuban origin of two specimens, now in the ANSP (where Parkes examined them), that died in the Philadelphia Zoo in the 1890's. We regard these specimens as insufficient evidence of the natural occurrence of *pratincola* on Cuba. A verified occurrence on Cuba was not unexpected, however; as Bond (1964) pointed out, some individuals of *pratincola* are known to travel great distances, and one banded as a juvenile in Pennsylvania was found dead in Key West, Florida, only 150 km from the nearest point in Cuba. Garrido (1978) has now published the particulars of a specimen of *pratincola* collected at

Monte Barreto, Marianao, Cuba, 1 October 1976, a date on which a major migratory movement of passerines was also noted in Marianao.

Turning now to the population of the Bay Islands, this may be called:

Tyto alba bondi, new subspecies

Holotype.—CM 131,548, male (presumably adult) from French Harbor, Isla Roatán, Bay Islands, Honduras, collected by A. C. Twomey on 7 April 1947 (field no. 11,967).

Characters.—To some extent intermediate in color between *T. a. pratincola* and *T. a. furcata*, but markedly smaller than either (see Table 1). The single male specimen is slightly paler dorsally than the palest of all *pratincola* examined. Its tail is almost pure white, with a single broken crossbar near the bases of the central rectrices; two pairs of small spots representing remnants of central and subterminal crossbars on these same rectrices; and slight freckling on all but the two outermost pairs of rectrices. The palest male *pratincola* seen (CM 6661, Virginia) has the outer pair of rectrices pure white, then the remainder increasingly marbled with dusky toward the central pair, which has two fairly distinct and two broken crossbars. All other *pratincola* seen had much more heavily pigmented tails. The inner web of the outer primary of the male *bondi* has three broken crossbars (the proximal two hardly more than spots), whereas in *pratincola* there are four to five, sometimes broken but more often solid. The outer web of this primary in *bondi* has some spots at the level of the crossbars of the inner web, and some dark speckling at the tip, but otherwise the outer web and the outer half of the inner web are pale buff, barely more than cream-colored. In *pratincola* the crossbars continue across the outer web, and there is also heavy speckling in most individuals, on a background varying from rich light buff to dark tawny. All but the innermost secondaries (=tertials) of the male *bondi* are almost pure white, with speckling on the outer web (extending to the inner web on the innermost of these white secondaries). There are two to three dark marks near the shafts of the secondaries, where *pratincola* has dark bars completely crossing the feathers. Even the palest *pratincola* (CM 6661) has much heavier speckling on the outer webs of these secondaries, such that the slightly darker (compared with *bondi*) background color is almost completely obscured. Most *pratincola* have even heavier speckling, often completely obscuring the dark ground color of the outer webs of the secondaries. All *pratincola* in the CM series except 6661 have the tips of the feathers of the facial disk rich red-brown to blackish; in 6661 these markings are of a faint orange-buff. In the male *bondi* there is no pigment on the tips of the feathers of the lower two thirds of the disk (these appear dark, but the feathers are adventitiously stained).

In comparison with *furcata*, the male *bondi* has the dark marbling of the back finer, with the teardrop-shaped markings of the back, scapulars, and tertials smaller and less contrasting. The rectrices have fewer markings and less of the buff wash than most males of *furcata*. The primaries are similar to those of *furcata*, but paler, with the crossbars fuscous rather than blackish, and tending to break up more. Almost all of the remiges of all but the palest extremes of male *furcata* have a faint to well-marked teardrop spot near or at the tip; in the male *bondi* these are present on only the four innermost secondaries. The outer webs of the secondaries in average male *furcata* have a ground color of pure white for about the basal one third to one half, becoming washed with buffy on the distal portion. In *bondi*, the white basal portion is confined to the area normally concealed by coverts, the remainder being of a uniform cream color. The facial disk of *furcata* is pigmented as in *pratincola*, unlike *bondi*. The spotting of the underparts of the male *bondi* is much sparser, with smaller spots, than most *furcata*, about as in *niveicauda*.

The two females of *bondi* differ *inter se*, that from Isla Guanaja being more heavily pigmented than that from Isla Roatán. The paler bird was compared in detail with the two palest females of *pratincola* in the CM series (137,714, Maryland, and 94,894, Florida). The general dorsal color of the two female *bondi* differs little if at all from *pratincola*, except that the teardrop marks are smaller and less conspicuous. In both *bondi* the two outermost pairs of rectrices are much paler than in *pratincola* females of similar underparts color. The paler *bondi* has the outer rectrix ground color pure white, the second outermost faintly washed with buff on the inner web. The outer rectrix of the pale bird has three fuscous spots rather than crossbars, these almost completely confined to the outer web. The darker *bondi* has a buff wash along the midline of the otherwise white outer rectrix, with two central spots and a broken subterminal crossbar. Even the palest-tailed female *pratincola* have at least an indication and usually strong crossbars on *both* webs of both of the two outermost rectrices, and none have any of these areas pure white—there is at least some wash of buff or pale fuscous. In darker *pratincola* females, the outer webs of the outer rectrices are no paler than the central rectrices, giving the whole tail a uniform ground color.

The primaries of female *bondi* are paler to much paler than those of *pratincola*, with smaller crossbars. The outermost primary of the paler *bondi* has the inner web ground color very pale buff, almost white. In the darker *bondi* it is a deeper buff, gradually paling to whitish buff at the inner margin. In even the palest *pratincola*, the outer half of the inner web is the same color as the outer web, and is sharply defined from the inner half of the outer web, which is white. The crossbars of the outer primary of the paler *bondi* number three plus a tiny spot at the shaft where the proximal crossbar would be. In the darker *bondi* there are four crossbars and in *pratincola* the number varies from four to five. The ground color of the secondaries is also paler to much paler than in *pratincola*. That of the inner webs is white in the paler *bondi*. In the darker *bondi* the ground color of the outer web, and also the crossbars, extend a few millimeters across the shaft to the inner web. In *pratincola* the ground color extends across the whole tip of the inner web, the white inner edge occupies half or less of the width of the inner webs of the secondaries, and the crossbars invade this white part.

The facial disk of the darker *bondi* consists of orange-buff feathers, those of about the lower third having small blackish tips. In the paler *bondi*, the disk feathers are white except for a few along the lower edge, which have narrow blackish tips. In *pratincola* the ground color varies, but the feathers of the lower half of the disk have well-marked black tips and a subterminal band of reddish brown.

In comparison with females of *furcata*, the marbling of the back of both of the *bondi* specimens is finer, so that less of the white ground color shows through, giving a blacker appearance to the dorsum of *bondi*. There is less difference in the teardrop spots than in the males, but those of *bondi* have the white centers rounder or more arrowhead-shaped, less linear. The primaries are much like those of *furcata*, but with more freckling on the outer web. Similarly, the secondaries are like those of *furcata*, but with darker crossbars and more freckling on the outer webs and tips. The facial disk feathers are not diagnostic in this instance, those of *furcata* being about midway between those of the paler and darker specimen of *bondi*. The spots on the underparts are fewer and smaller than in *furcata*, but somewhat larger and more abundant than in the female *niveicauda*.

Range.—Known only from Islas Guanaja and Roatán, two of the three largest of the Bay Islands, off the Caribbean coast of Honduras.

Remarks.—It is a pleasure to name this distinctive form for our friend James Bond of the Academy of Natural Sciences of Philadelphia, collector of the first Bay Islands specimen of Barn Owl, whose

interest in the Caribbean Islands has long included those of the periphery, such as Isla Cozumel, the cays off Belize, and the Bay Islands.

It is unlikely that the difference in color between the Guanaja and Roatán females represents geographic rather than individual variation. In the only species that is known to show geographic variation *within* the Bay Islands, *Melanerpes aurifrons*, the populations of Isla Utila and Isla Roatán were obviously derived from two rather different mainland subspecies groups (Monroe, 1968:214). Monroe (1968:399) listed 29 resident land bird species from the Bay Islands; two of these are based on single, probably mislabeled specimens (Phillips, 1970). Of the 27 remaining species, Monroe recognized endemic Bay Islands subspecies for six, with the Barn Owl now making a seventh. Monroe apparently did not examine Bond's Isla Guanaja Barn Owl, as he erroneously stated (1968:154) that all of the Bay Islands specimens are "white-phase birds." His statement that Bay Islands Barn Owls are "indistinguishable from North American specimens" is, of course, also erroneous as demonstrated in the present paper.

Bond's specimen is of special interest to students of molt. It was a breeding bird—a note on the label reads "shot at nest while carrying rat to young." It is, however, actively molting flight feathers, and there are also scattered sheathed body feathers. At least some of the primaries and secondaries are partly grown, but the exact number would be difficult to determine without damaging the specimen. On the right side of the tail, rectrix 6 (outermost) is old, 5 about two thirds, 4 about three quarters, 3 old, 2 about three quarters grown, and 1 about seven eighths grown. On the left side, rectrices 6, 5, 3, 2, and 1 are old, and 4 about two thirds grown. Stresemann and Stresemann (1966:373) stated that most molting *Tyto alba* that they had examined had only one or two rectrices growing at any one time, and they found none with more than three. The Isla Guanaja specimen was growing four new rectrices on the right side and one on the left.

Neither Payne (1969) nor Foster (1975) mentioned owls in their surveys of molt/breeding overlap in tropical birds, but Payne later (1972) suggested that females of the far northern strigid owls *Nyctea scandiaca* and *Surnia ulula* "may molt soon after egg-laying."

REMARKS ON MIDDLE AMERICAN MAINLAND POPULATIONS

Carnegie Museum of Natural History has a male Barn Owl taken at Los Planes, in the coastal lowlands of Honduras, and a supposed pair from Siguatepeque, at about 1,000 m elevation in the interior, all collected by A. C. Twomey and R. W. Hawkins. Monroe (1968:154) wrote of the lowland male that it "is a white-phase individual matching *pratinctola*." It indeed matches male *pratinctola* in color, but has decidedly

shorter wings and tail, matching the Isla Roatán male fairly closely in this respect. Monroe assigned all Barn Owls from the interior of Honduras, including the CM specimens from Siguatepeque, to *T. a. guatemalae* (Ridgway). Although Twomey and Hawkins sexed these as a pair, this must be regarded as dubious. Both are "dark-phase" birds, and the supposed male is indeed slightly paler than the female. However, the measurements of the two are almost identical, with the "male" having a wing *longer* than that of the female, and matching males of *pratincola*, whereas the female is decidedly smaller than females of *pratincola*. The color differences between these two specimens are well within the normal range of variation shown by females of other subspecies, and, in fact, the two are more alike than are the two females of *bondi*. Enough other missexed specimens have been found among the Honduran birds taken by Twomey and Hawkins to make quite reasonable the assumption that both of the Siguatepeque birds are, in fact, females. Given this assumption, the three CM Honduras specimens are all smaller than *pratincola*, and the plumage and size differences between the Los Planes male and the two Siguatepeque females are quite compatible with the degree of sexual dimorphism shown in other populations. It is likely that the mainland of Honduras is inhabited by only a single subspecies of *Tyto alba* rather than two as postulated by Monroe. This would presumably be *T. a. guatemalae*, but the status of that supposed subspecies needs reexamination.

According to Wetmore (1968:146), "The race *Tyto a. guatemalae* ranges from western Guatemala through southern Central America, to northern Colombia. It differs from *Tyto alba pratincola* of North America and northern Central America only in having slightly darker color." Bond (1936), however, as quoted earlier, stated that *pratincola* of North America "is known to range south to eastern Nicaragua." Friedmann et al. (1950:137) gave the range of *pratincola* as south "to eastern Guatemala and probably eastern Nicaragua." They did not mention *guatemalae*, thus apparently either overlooking or rejecting the identification of a female specimen from Jalapa, Veracruz, Mexico, as *guatemalae* by Davis (1945), who wrote "It is darker both dorsally and ventrally than *pratincola* from southern Texas, Nuevo León, and the Valley of México, and matches the lighter-colored specimens of *guatemalae* from Central America in the Biological Survey Collection. This record extends considerably northward the known range of this race." On the other hand, Lowery and Dalquest (1951) wrote of their male from Potrero Viejo, Veracruz (about 150 km SSE of Jalapa): "This specimen is virtually indistinguishable from light-phased examples from the United States, thereby excluding the possibility of its being referable to *Tyto alba guatemalae*." Alvarez del Toro (1964)

assigned the Barn Owls of Chiapas, the southernmost state of Mexico (adjacent to Guatemala), to *T. a. pratincola* without comment.

At the southern end of the putative range of *guatemalae*, its ascription to northern Colombia by Meyer de Schauensee (1949) is based on a letter from Wetmore quoted by Dugand (1945), in which a specimen from Los Pendales, Atlántico, as well as the "Bogotá" trade skin holotype of *T. a. subandeana* Kelso were stated to be inseparable from what Wetmore called the "quite rare" light phase of *guatemalae*.

Wetmore's measurements of *guatemalae* (1968:145) were taken from a series of 10 males and 10 females from Guatemala, El Salvador, Nicaragua, Costa Rica, and Panama. Combining measurements from this large area obscures what appears to be geographic variation in size. This is indicated by measurements taken for this study, as follows: Honduras—♂ wing, 314, tail, 111.5, and ♀ wing, 326, 331, tail, 129, 129; Nicaragua—♂ wing, 324, 327, 329, tail, 116, 123, 125, and ♀ wing, 329, 339, 350, tail, 129, 136, 140 [Nicaragua series includes some sexed inferentially]; Costa Rica—♂ wing, 333, tail, 129, and ♀ wing, 332, 332, tail, 130, 133; Panama—♂ wing, 313, 315, tail, 119, 121, and ♀ wing, 310, tail, 125.

Several points are of interest in this list of measurements. The Honduras lowland male is markedly small in comparison with the cotypes of *guatemalae* (as designated by Deignan, 1961:138) and other specimens from Nicaragua, but the highland females match the smallest Nicaragua females. Costa Rica specimens match those from Nicaragua reasonably well, but those from Panama are tiny. The few measurements given by Ridgway (1914:610) match this pattern. A larger series would be required to verify the seeming lack of size dimorphism in Costa Rica and Panama.

Direct color comparisons were made at AMNH among two Nicaragua (Matagalpa), three Costa Rica, and two Panama specimens of *guatemalae*. Among these, the Nicaragua specimens were darker and blacker dorsally than the Costa Rica, with a darker tail bearing wider black bands. The Panama specimens were nearest the Costa Rica in dorsal color. Ventrally, the Costa Rica and Panama females were very dark in ground color; one Costa Rica (Nicoya) and the single Panama (Agua Dulce, Coclé) female were heavily marked below, the second Costa Rica female (San José) relatively lightly spotted. The Costa Rica male (Las Cañas, Guanacaste) was very pale, almost white, and lightly spotted below; that from Panama (Almirante, Bocas del Toro) medium buff below but with abundant small spots. Nicaragua specimens (AMNH and USNM) are all buffy below, usually with rather heavy spotting. Those thought to be males on the basis of measurements are consistently less heavily pigmented than those thought to be females, agreeing with the few sexed specimens from this country. Except for

the whitish Costa Rica male, *underparts* color of Panama and Costa Rica specimens did not differ significantly (that is, within the normal range of variation of a subspecies of *Tyto alba*) from the Nicaragua series.

Dickey and van Rossem (1938:225) stated that "there is some evidence that *guatemalae* may be only a dark phase of the common North American barn owl, for a Sonora specimen in the Dickey collection is apparently identical with El Salvador birds." The "dark phase" Central American specimens are not only of a rich dark buff on the underparts, but have heavier ventral markings than most "dark phase" *pratincola* from the United States, with a strong tendency for the development of linear streaks and crossbars rather than merely dots on individual feathers. Even the pale males from Central America tend to show some narrow linear streaks, especially along the flanks, not seen in typical males of *pratincola*. However, California and western Mexico specimens of *pratincola* show a strong tendency toward dark ventral markings of the kind typical of *guatemalae* (examples include AMNH 360,333 from Witch Creek, San Diego Co., and 476,476 from Los Angeles). The measurements of Nicaragua and Costa Rica specimens of *guatemalae* match well those of a series of 21 from the Pacific Coast (20 California, one Oregon). The California series as a whole could be considered to be intergrades between *pratincola* and *guatemalae*, were it not for the small Honduras specimens from an area between the range of *pratincola* and the type locality of *guatemalae* (Chinandega, Nicaragua; the name "*guatemalae*" was admitted by its author to have been a *lapsus*, as he had seen no Guatemala specimens [Ridgway, 1914:610]).

It should be clear from the above remarks that the taxonomic status of the Barn Owls of the Pacific coast of the United States and of all of Middle America south to northern Colombia needs a thorough investigation, assembling all available material, and analyzing *both* size and color, keeping sexual dimorphism in mind for both. Neither the characters nor the geographic range of "*guatemalae*" have ever been satisfactorily determined.

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ARTICLE 21

CTENOSPONDYLUS NINEVEHENSIS, A NEW SPECIES (REPTILIA, PELYCOSAURIA) FROM THE LOWER PERMIAN DUNKARD GROUP OF OHIO

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ABSTRACT

A new species of spenacodontine pelycosaur, *Ctenospondylus ninevehensis*, is described on the basis of disarticulated elements of the skull and postcranial skeleton from the Lower Permian Greene Formation, Dunkard Group of east-central Ohio. This is only the second species of this rare genus to be recognized and the first to be reported from the eastern United States. *C. ninevehensis* existed at the same time or very probably somewhat later than *C. casei*, the other member of this genus, yet its greater primitiveness in a number of features makes it an ideal predecessor to *C. casei*. Geographic isolation by the end of the Pennsylvanian of the Dunkard basin, in which *C. ninevehensis* occurred, from the Midcontinental basin complex, in which *C. casei* occurred, is offered as a possible explanation for the anachronistic appearance of the former. *Ctenospondylus* was most likely already established as a distinct lineage before the beginning of the Permian and, therefore, not a descendant of any of the Early Permian spenacodontines, such as *Sphenacodon*. It is also improbable that *Ctenospondylus* could have arisen from any of the few poorly known spenacodontines of the Late Pennsylvanian because of the greater primitiveness of the marginal dentition of *C. ninevehensis*. For these reasons it seems best to take the view that *Ctenospondylus* arose from the haptodontine spenacodontids at least as early as the Late Pennsylvanian.

INTRODUCTION

Reptiles of the Lower Permian subfamily Sphenacodontinae are considered the most advanced of the order Pelycosauria and closest to the morphological grade of organization of the therapsids, the advanced mammal-like reptiles. *Ctenospondylus* is one of the rarest of the better

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known sphenacodontine pelycosaurs and previously was recognized by only one species, *C. casei*, recorded from only two regions in the United States, north-central Texas and southeastern Utah. It is distinguished from other members of this group mainly by its long, laterally flattened, neural spines that form a high dorsal sail. In addition to *Ctenospondylus*, four other genera comprise the sphenacodontines as follows: *Bathygnathus*, known only from the front part of a skull found on Prince Edward Island, Canada, may be a senior synonym of *Dimetrodon* (Langston, 1963); *Neosaurus*, based on a maxilla from the Jura region of France; *Sphenacodon* and *Dimetrodon*, known from complete skeletons from North America and an upper jaw of the former from England (Paton, 1974). The holotype of *C. casei*, discovered by W. F. Cummins in 1881 in the Lower Permian Belle Plains Formation, Wichita Group of north-central Texas, consists of a complete dorsal vertebra, a dorsal vertebra with partial neural spine, a cervical vertebra lacking the spine, a probable cervical spine, the distal part of a spine, and several fragments of ribs. This specimen was not noted until 1910, however, when Case referred briefly to it and suggested that it be assigned to the European Lower Triassic genus *Ctenosaurus* Huene, a reptile known only from its vertebral column in which the spines are greatly elongated as in *Ctenospondylus*. About a quarter century later the uniqueness of this specimen was recognized by Romer (1936), who named *Ctenospondylus casei*. Further remains of *C. casei* went unreported until Vaughn (1964) discovered many skeletal elements referable to this species in the Lower Permian Organ Rock Shale, Cutler Group of southeastern Utah. Vaughn's descriptions (1964, 1970) included not only portions of the postcranial skeleton, but also, most importantly, the skull. The skull is nearly identical to those of *Sphenacodon* and *Dimetrodon* and provides indisputable evidence that *C. casei* is a sphenacodontine, as well as that it is closely related to these genera.

The specimens described here from the Lower Permian Greene Formation, Dunkard Group of east-central Ohio were first noted by Olson (1975), who referred them to the genus *Ctenospondylus* without specific designation. Examination of the Dunkard *Ctenospondylus* reveals that it represents a new species, herein named *C. ninevehensis*, and that it is more primitive than the contemporaneous, or very likely somewhat earlier, *C. casei*. Despite its late appearance, *C. ninevehensis* is viewed as an ideal, structural antecedent to *C. casei*.

The ancestry of *Ctenospondylus* remains vague. Of the Lower Permian sphenacodontines, only *Sphenacodon*, *Dimetrodon*, and *Ctenospondylus* are known from complete or substantial portions of their skeletons, which are essentially identical except for their distinctly different neural spines. In all three genera the spines are elongated; in *Dimetrodon* the spines are flattened laterally at their bases only, becoming very

long, slender rods distally, whereas the spines of *Ctenospondylus* are intermediate in length between those of *Dimetrodon* and *Sphenacodon* and, as in the latter, have a basically normal, blade-like structure. It might be suggested that the longer-spined *Ctenospondylus* was derived from the shorter-spined *Sphenacodon* as a result of the well-documented evolutionary trend toward disproportional increase in spine length with increase in overall size seen not only in the latter, but in other pelycosaurs as well. A *Sphenacodon-Ctenospondylus* lineage cannot be correct, however, because *C. ninevehensis* possesses a more primitive dentition than the oldest and most primitive species of *Sphenacodon*. Features of the maxillary dentition of *Neosaurus* suggest that this poorly known genus was also not ancestral to *Ctenospondylus*. Probably *Ctenospondylus*, as well as *Sphenacodon*, represented independent lineages during the Early Permian. The few incompletely known sphenacodontines of the Late Pennsylvanian are also eliminated as possible ancestors of *Ctenospondylus* because of their more advanced dentitions than that of *C. ninevehensis*. It is suggested that *Ctenospondylus* became established as a separate evolutionary line by the Late Pennsylvanian or earlier, most likely stemming from the Late Pennsylvanian-Early Permian haptodontine pelycosaurs, which are generally considered as ideal predecessors of the sphenacodontines and as probably having an antiquity that extends back to the Early or Middle Pennsylvanian.

The greater primitiveness of *C. ninevehensis* over the contemporaneous or probably earlier-occurring *C. casei* is explained as the result of isolation. Paleogeographic reconstructions suggest that the Dunkard basin, once the terminal portion of a northeastern arm of the Midcontinental seaway, became widely separated from the Midcontinental basin complex at the end of the Pennsylvanian by the continued growth of a vast, intervening area of low relief occupying the continental interior.

The following abbreviations are used to refer to repositories of specimens: AMNH, American Museum of Natural History, New York; NTM VP, Navajo Tribal Museum, Window Rock, Arizona; MCZ, Museum of Comparative Zoology, Harvard University.

SYSTEMATIC PALEONTOLOGY

Class Reptilia

Order Pelycosauria

Family Sphenacodontidae

Subfamily Sphenacodontinae

Genus *Ctenospondylus* Romer, 1936

Ctenospondylus ninevehensis, new species

Holotype.—MCZ 3386 consists of the following disarticulated elements of the skull, lower jaw and postcranial skeleton: premaxillae, left

maxilla and small part of right, right prefrontal, probable right jugal, left pterygoid, left dentary, axial neural spine, three dorsal vertebrae and spine, lumbar vertebra, four caudal vertebrae and probable spine, three cervical ribs and parts of cervical and dorsal ribs, part of scapular blade, left humerus and distal end of right, and right pelvis. The holotype, as well as the referred specimen, were collected by Dr. Donald Baird of Princeton in June 1955.

Referred specimen.—MCZ 4458, a right maxilla.

Horizon.—Lower Permian Nineveh Limestone, Greene Formation, Dunkard Group.

Locality.—Clark Hill on County Route 43, 1.1 miles west of junction with State Route 7, sec. 16, Salem Township, Monroe County, Ohio.

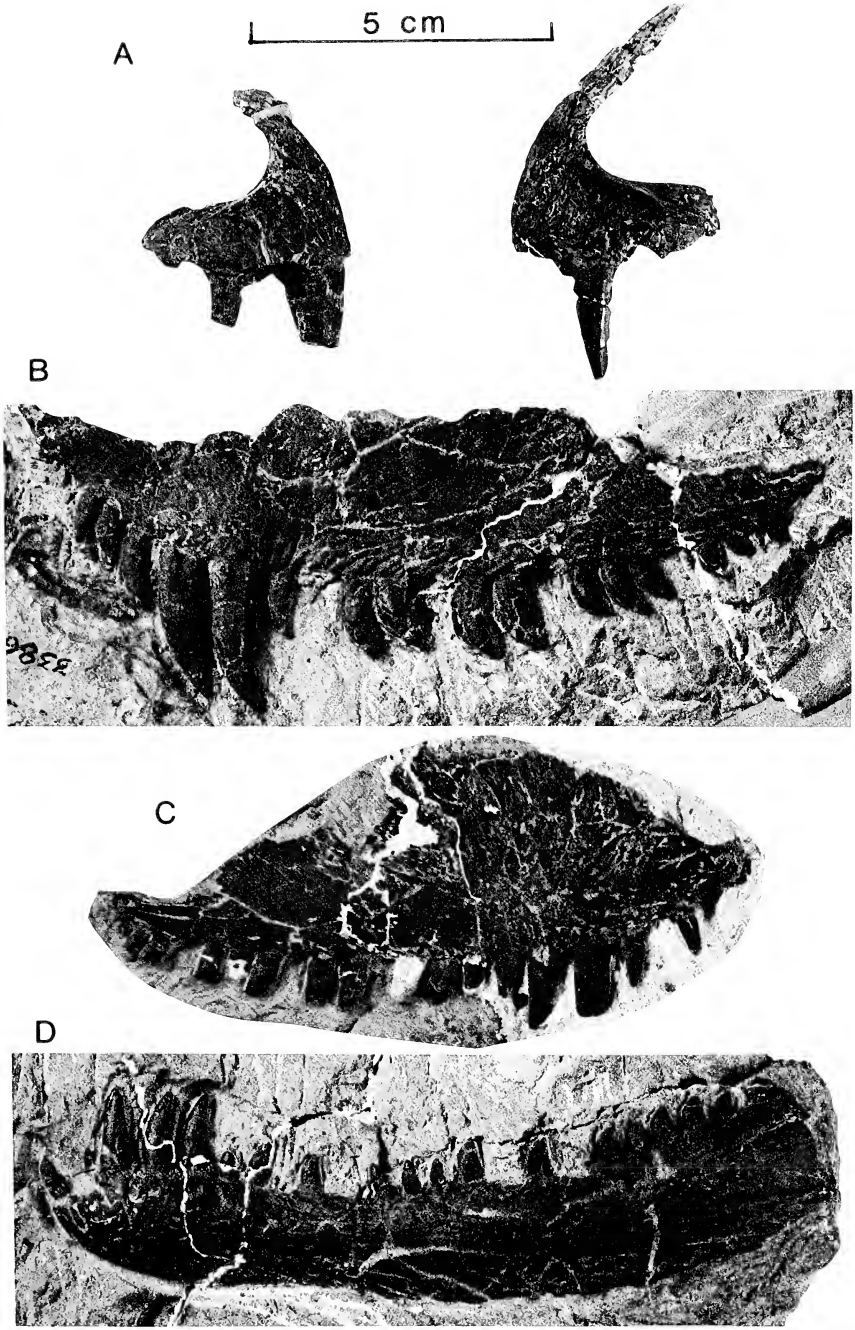
Diagnosis.—All the features that distinguish *Ctenospondylus ninevehensis* from *C. casei* express a more primitive grade of organization in the former; these include: 1) a greater number of marginal teeth, consisting of four premaxillary, 21 maxillary, including three precanines, and an estimated 31 dentary teeth; 2) relative length of neural spine of dorsal vertebra about 23% shorter; 3) axial neural spine of the more generalized spenacodontine shape; 4) smaller overall body size.

Etymology.—Name refers to the stratigraphic unit in which the specimens were found.

Description

Cranial elements.—Cranial elements of the holotype include right and left premaxillae, left maxilla and small part of right, right prefrontal, probable right jugal, left pterygoid, and left dentary. The reasons for believing that these elements, as well as those described below as belonging to the holotype, came from one individual is their discovery close together, their appropriateness in size to one another, and the absence of duplicate elements of the same size or evidence of the presence of any additional pelycosaur species. A right maxilla, MCZ 4458, is also referred to *C. ninevehensis*. Both the right and left premaxillae (Fig. 1) are nearly complete and possess spaces for four teeth, which is one or two more than is seen in most of the spenacodontine pelycosaurs. The teeth appear to have been alternately replaced, so that only two functional teeth are present in each premaxilla; further, the tooth replacement sequence of one premaxilla alternates with that of the opposite side. In the right premaxilla only the basal halves of the first and third teeth are preserved and the second and fourth are represented by empty sockets, whereas in the left the second tooth is nearly intact, the fourth has been broken off at the base and the first and third sockets are empty except for the tip of a replacement tooth seen in the third. Judging from what is preserved of the functional teeth and the sizes of the unoccupied sockets, the size relationships of the premaxillary teeth are of the typical spenacodontine pattern; the teeth decrease in size considerably posteriorly, with the anterior pair being much larger than the posterior pair. The teeth

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Fig. 1.—*Ctenospondylus ninevehensis*, new species A, right and left premaxillae, B, left maxilla, and D, left dentary of holotype MCZ 3386. C, right maxilla of referred specimen MCZ 4458.



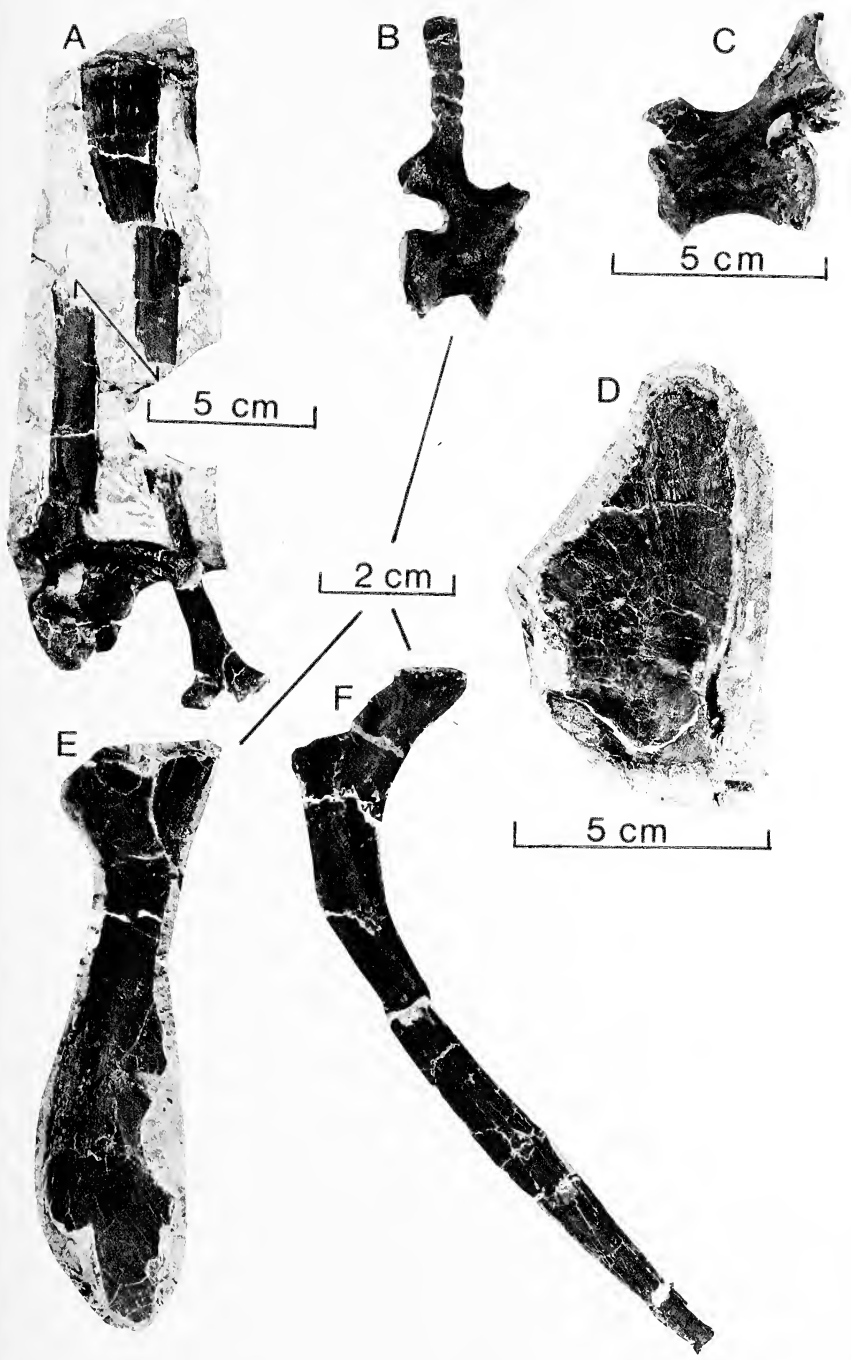
are subcircular in cross-section and exhibit only a slight development of anterior and posterior cutting edges. The holotypic left maxilla (Fig. 1) is complete along its lightly convex, ventral margin and has a maximum length of 133 mm; the upper half of its dorsal lamina is missing. Sixteen teeth are preserved and there are spaces for five more, giving a total of three precanines, two canines, and 16 postcanines. The precanines decrease in size anteriorly from a maximum length of 14 mm; the canine pair are nearly equal in size and measure 25 mm in length; the first postcanine is slightly smaller than the posteriormost precanine and the second postcanine (missing) is presumed to have been smaller as in the referred right maxilla MCZ 4458 (Fig. 1); the remaining postcanines exhibit a steady decrease in size posteriorly from a maximum length of about 13 to less than 4 mm. In sphenacodontid fashion all the teeth are slightly to moderately recurved and laterally compressed with moderately developed, nonserrated, posterior cutting edges; postcanines 8 through 21 are slightly bulbous compared to the other teeth. There is a moderate swelling of the maxilla above the canine pair and anterior to the precanines the ventral margin of the maxilla is only very slightly arched dorsally, forming a very weakly-developed maxillary "step." The referred right maxilla MCZ 4458 (Fig. 1) is essentially complete and except for a couple of very minor differences that are undoubtedly related to its smaller size (length 106 mm) is identical to that of the type. The two canines appear to be relatively slightly smaller, with the anterior one, though not complete, being definitely larger; its maxillary step and lateral canine swelling are also less pronounced than in MCZ 3386.

The holotypic right maxilla is represented by only a small, poorly preserved portion of its anteroventral margin that contains a canine pair and a precanine that match exactly in size and character those of the left maxilla. The greater portions of the right prefrontal and what appears to be a right jugal exposed in medial view are preserved and are not unlike those of other sphenacodontines. All that remains of the left pterygoid is the proximal portion of the palatal ramus and almost all of the thickened, ventral ridge of the quadrate ramus. The transverse flange is well developed with five of the 10 or more teeth it possessed preserved; the largest of these teeth, located at the center of the series, is about 8 mm in length. The palatal ramus is covered by very small denticles; however, about 15 mm anterior to the transverse flange and close to the medial border of the palatal ramus begins a narrow cluster of relatively much larger denticles, reaching a maximum diameter of about 1.7 mm, that extends about 10 mm to the anterior broken margin of the pterygoid. In all these features the pterygoid of the holotype closely approximates that seen in the reconstruction of the skull of *Dimetrodon limbatus* by Romer and Price (1940:501, Pl. 13).

The left dentary (Fig. 1) as preserved measures 125 mm in length and is missing approximately its posterior fourth, which undoubtedly included a small part of the marginal dentition. The tooth-bearing margin of the dentary is slightly concave except at its very anterior end, where it slants somewhat downward. There are 19 preserved teeth of which only the posteriormost two are incomplete and there are gaps for six more. The total number of marginal dentary teeth was, however, almost certainly greater than 25, judging from the dental counts given by Romer and Price (1940:434, Table 2) for specimens of various species of *Sphenacodon* and *Dimetrodon*. The dental counts in-

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Fig. 2.—*Ctenospondylus ninevehensis*, holotype, MCZ 3386. A, posterolateral view of anterior dorsal vertebra (displacement of spine indicated) and posterior view of proximal half of spine of a preceeding dorsal; B, right lateral view of mid-caudal vertebra; C, left lateral view of distal caudal; D, left lateral view of axial neural spine; E, anterior view of atlantal or possibly axial rib; F, posterior view of left cervical rib.



dicate that in sphenacodontines the dentary typically possesses about 50% more teeth than the maxilla. On the basis of this formula, the presence of 21 teeth in the maxilla of the Dunkard *Ctenospondylus* suggests that the actual number of dentary teeth may have been about 31. All the teeth are slightly to moderately recurved and laterally compressed with fairly sharp, nonserrated, posterior edges. In sphenacodontine fashion there are a few teeth very near the anterior end of the jaw that are much enlarged over the rest of the series. In this case three enlarged teeth of essentially identical development and measuring 13 mm in length occupy positions 3, 4, and 5. Missing tooth 2, judging from its empty socket, must have been somewhat larger than tooth 1, which measures 8 mm in length; that part of the series containing teeth 6 to 14 shows great variation in size, with teeth ranging in length from 5 to 8 mm; teeth 15 to 25 diminish slightly in size posteriorly from a maximum length of 7 mm and exhibit a slightly stouter outline than the other teeth of this size range.

Vertebrae and ribs.—Elements of the vertebral column identified as belonging to MCZ 3386 include an axial neural spine, three dorsal vertebrae and a dorsal neural spine, a lumbar vertebra, four caudal vertebrae and a probable caudal neural spine, and three cervical ribs and parts of cervical and dorsal ribs. The axial neural spine (Fig. 2) is essentially complete, exposed in left lateral view and includes a small, proximal portion of the anterior and most of the posterior zygapophyses of this side. In outline the spine conforms very closely to those of *Sphenacodon* and is also not greatly unlike those of various species of *Dimetrodon* (Case and Williston, 1913; Romer and Price, 1940; Vaughn, 1964). In comparison with these genera the holotypic spine differs mainly in not becoming greatly thickened toward its posterior margin. The height of the spine is about 74 mm measured above the posterior zygapophysis along a line parallel to its posterior edge. In sphenacodontid fashion the anteroventral margin projects over the anterior zygapophysis, from which it is separated by a narrow, deep notch.

The three vertebrae and neural spine from the dorsal region of the column include a complete vertebra and the proximal half of a spine found closely associated with it (most likely belonging to the preceding vertebra) that are probably from the anterior part of the series (Fig. 2) and two vertebrae, consisting mainly of the centrum and the base of the neural spine, believed to be from the middle and posterior parts of the series. All are of sphenacodontid style. The lateral surface of the neural spine just above the transverse process is deeply excavated. The zygapophyses are steeply tilted downward and inward and do not extend laterally beyond the margin of the centrum. The lateral surface of the centrum is deeply concave, flaring outward at the ends of the centrum to form an expanded, subcircular rim surrounding the notochordal funnel. The ventral longitudinal keel of the centrum is sharply pinched and in lateral view is slightly concave, reaching the ventral margins of the centrum rims, which are expanded downward as relatively flat lips for articulation with the intercentra. The dorsals, as well as the lumbar and caudal vertebrae described below, exhibit well developed anterior centrosphenes and posterior centrantra on the dorsal margins of the centrum rims. In all of the vertebrae there is also a ventral beveling of the ends of the centra to accommodate the intercentra; this feature, which is much more pronounced at the anterior end of the centrum, becomes less prominent toward the posterior end of the column. Standard measurements for the vertebrae of the holotype are given in Table 1.

The preservation of the complete anterior dorsal vertebra (Fig. 2) is fortunate inasmuch as it is the character of the neural spine that provides the basis for identifying the holotype as belonging to the genus *Ctenospondylus*. Although two parts of the neural spine have been displaced small distances along fracture planes, the height of the spine above the posterior zygapophyses can still be accurately measured as 152.4 mm. The spine is laterally compressed, with an anteroposterior length of about 14 mm from just above the buttresses of the posterior zygapophyses to about a third the height of the spine, then constricts to about 12 mm for a very short distance before slowly expanding

Table 1.—Measurements (in mm) of various vertebrae of *C. ninevehensis*, holotype, MCZ 3386; dorsal vertebrae of *Ctenospondylus* aff. *C. casei*, NTM VP 1014 from southeastern Utah (Vaughn, 1964); and *C. casei*, holotype, AMNH 4047 from north-central Texas (Romer and Price, 1940). 1, greatest length of centrum; 2, width of centrum at posterior end (anterior end for NTM VP 1014); 3, height of centrum at posterior end; 4, orthometric linear unit value (radius of centrum to the $\frac{2}{3}$ power; see Romer and Price, 1940); 5, spine length; 6, spine length in orthometric linear units.

Specimen and vertebrae	1	2	3	4	5	6
MCZ 3386						
anterior dorsal	24.5	21.3	24.3	4.8	152.4	31.7
mid-dorsal	27.2	20.0	20.0	4.6		
posterior dorsal	27.0	13.7	22.2			
lumbar	19.5	15.5	14.7			
proximal caudal	18.0	15.9	16.0			
proximal caudal	17.6	15.5	14.2			
mid-caudal	18.0	14.8	13.8			
distal caudal	17.0	10.0	9.5			
NTM VP 1014		22.0		4.9	211.0	42.5
AMNH 4047	34.0	31.0	33.0	6.2	245.0	40.0

to 23 mm at its distal end. In transverse width the spine is about 10 mm just above the buttresses of the posterior zygapophyses and 8 mm at its summit. The basal third of the spine bears fore and aft grooves and ridges, which appear to be more pronounced on the anterior face; at about the level where the spine is narrowest anteroposteriorly these grooves are replaced by rounded margins. The transverse process is well developed and extends 40 mm laterally out from the midline, is directed slightly downward and backward, is roughly triangular in cross section with the apex directed downward, is broadly concave ventrally in end view, and exhibits a rather deep excavation on the posteroventral surface of its base. The articular facet is egg-shaped in outline with the narrower end pointing ventrally and faces ventrolaterally and slightly posteriorly. The line of juncture between the arch and centrum is detectable only as a roughened ridge. By way of comparison with the vertebra described as an anterior dorsal, the vertebra believed to be a mid-dorsal is judged so by differences in its transverse process. The process is shorter, measuring 32.7 mm out from the midline, and extends directly laterally. Its articular facet is triangular in outline with the apex pointing downward and faces ventrolaterally; the apex of the facet is formed by the end of a thin ridge that extends along the ventral length of the process. The presumed posterior dorsal vertebra has undergone lateral crushing, which is most obviously reflected in its relatively very narrow centrum width. The transverse process is short, about 5 mm, and in cross section is narrowly oval with anteroposterior elongation. Its articular facet is also oval and faces laterally and very slightly ventrally. A slightly raised, subcircular facet for the capitulum of the rib is seen high up on the anterior rim of the centrum.

The single, presumed lumbar vertebra consists essentially of the centrum and the base of the neural spine. The base of the spine is about 8 mm in anteroposterior length and is only very slightly excavated laterally. The transverse process, or diapophysis, is positioned on the upper half of the centrum, is oval in cross section with its long axis directed anterodorsally, and projects outward from the centrum just barely at its anterior edge to about 5 mm at its posterior edge. Its oval articular surface extends from a point near the upper margin of the anterior rim of the centrum posteroventrally to a little

beyond the mid-length of the centrum and faces laterally and slightly anteriorly. The parapophysis is considerably smaller than the diapophysis, appears as a slightly raised, vertically elongated oval area located beside the anterior rim of the centrum and is separated from the diapophysis by a very narrow channel for the passage of the segmental artery; its articular surface faces ventrolaterally. The lower half of the lateral surface of the centrum is lightly excavated and the ventral, longitudinal keel is weakly developed.

The four caudal vertebrae of the holotype include two from the proximal and one each from the middle and distal regions of the tail. The proximal caudals consist for the most part of the centrum and the base of the spine. The spines are laterally compressed and only slightly excavated at their bases. In anteroposterior length the spine of the larger vertebra is 9 mm, whereas that of the smaller one is about 7.3 mm. Enough of the spines are preserved to indicate that they were inclined slightly anteriorly. In both proximal caudals the transverse processes are for the most part preserved and probably include very small portions of the fused ribs. The process has a broad base, extending across the upper half of the centrum from the anterior rim to within a short distance of the posterior rim, and projects ventrolaterally. A well-developed ridge extends upward from the lateral edge of the anterior rim of the centrum to buttress the process along the anterior margin of its ventral surface. The mid-caudal vertebra (Fig. 2) lacks essentially only the posterior zygapophyses and portions of the anterior zygapophyses. The neural spine is about 24 mm high, measured above the posterior zygapophyses, is moderately excavated at its base, and curves very slightly posteriorly. In anteroposterior length the spine is 5.2 mm just above the buttresses of the posterior zygapophyses, then gradually expands to 5.7 mm at its termination. The transverse process is reduced to a low protuberance high up on the centrum and somewhat anterior to its mid-length; posterior to the process is a rather deep, dimple-like depression. The incompletely preserved ventral keel of the centrum is represented by a low ridge. The distal caudal vertebra (Fig. 2) is complete except for the tip of the spine and very small portions of the anterior zygapophyses. The spine is inclined slightly posteriorly and tapers to what was probably a blunt point. Excavation of the neural arch at its base is reduced to a slight depression and the median ventral keel or ridge has been replaced by a narrow, flat surface. An isolated, laterally flattened neural spine that is complete to just below the posterior zygapophyses but incomplete distally has been catalogued with the holotype as probably belonging to a proximal caudal. As preserved it extends 23.4 mm above the posterior zygapophyses, has an anteroposterior length of 7.8 mm just above the buttresses of the zygapophyses, but expands distally to about 10.2 mm.

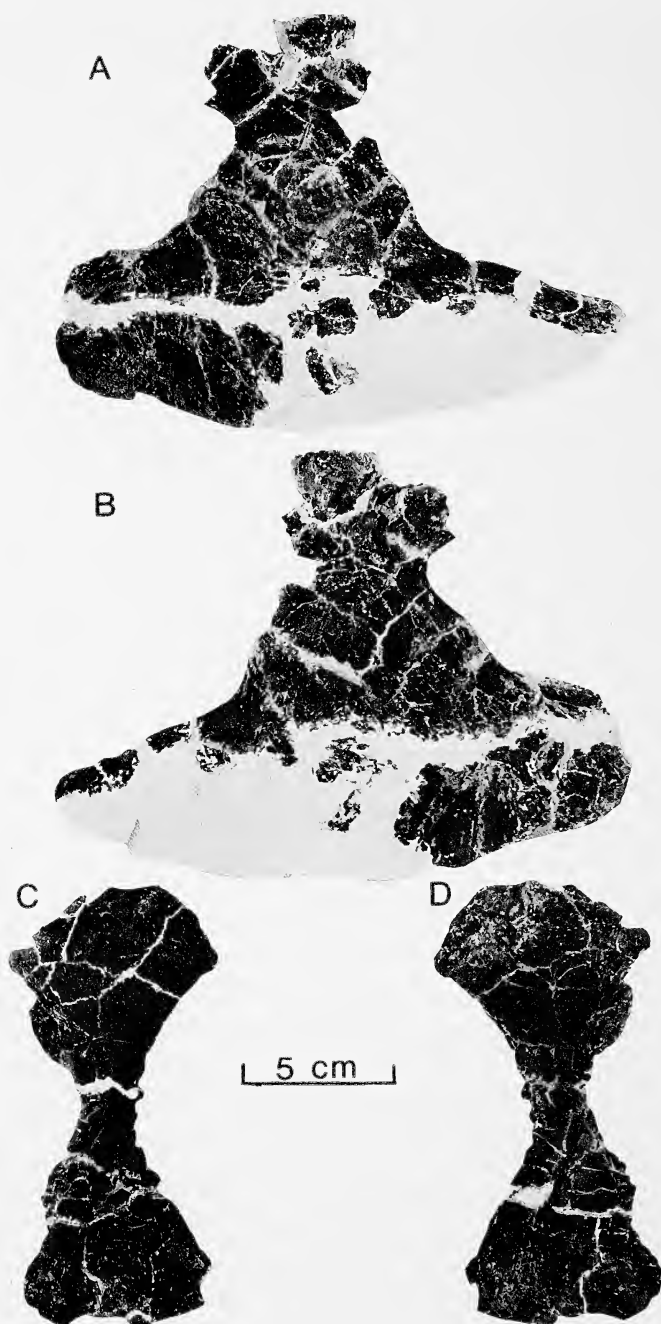
One of the three complete or nearly complete cervical ribs (Fig. 2) of MCZ 3386 is suspected of belonging to the atlas or possibly the axis. In this rib the capitulum and tuberculum appear to be about equally developed, are set close together, and meet at an angle between them of about 35°. There is a small gap in the triangular sheet of bone connecting the two heads that is probably due to imperfect preservation and the rib can, therefore, be described as holocephalous. Unusual is the very thin, paddle-like expansion of the distal portion of the rib shaft. Romer and Price (1940) point out that in ophiacodonts there is some development of a flat, paddle-like blade of the cervical rib shaft for attachment of the levator and anterior serratus muscles supporting the scapula; they also see some evidence of a similar condition in edaphosaurs. Further, their figures (Romer and Price, 1940:299, Fig. 58) of the primitive spenacodontid *Haptodus* show a distal dialation of the anterior cervical ribs. However, they state that among the more advanced spenacodontids there is no distal expansion of the cervical ribs. They note that the first seven cervicals of *Dimetrodon* end in pointed tips, but do not comment on *Sphenacodon*, for which this information is apparently lacking. It is interesting that Vaughn (1964) has described a fragmentary cervical rib in *Ctenospondylus* that is somewhat expanded distally. As preserved the presumed axial or atlantal cervical rib of *C.*

ninevehensis is 81 mm long, 19.8 mm wide at its proximal end, 8.8 mm wide at its narrowest point just distal to the union of the rib heads, and about 19 mm across the widest point of its distally expanded shaft. Because the distal portion of the rib is incompletely preserved, the actual maximum width and length of the rib are at least slightly greater than the measurements given above. Although the proximal ends of the other two cervical ribs (Fig. 2) are somewhat incomplete, they also appear to be at least nearly holocephalous. Their shafts are essentially complete and are typically sphenacodontid in being slender and oval in cross-section, and in having pointed ends. The smaller and presumably more anterior of the two ribs is 105 mm long, 27.8 mm wide at its proximal end, and about 8 mm wide at about mid-length of the shaft; the same measurements for the larger rib are 131, 26, and 8 mm respectively. Among the materials assigned to MCZ 3386 are portions of rib shafts and a poorly preserved proximal end of a dichoccephalous rib that was undoubtedly from the dorsal region of the column.

Appendicular elements.—All that remains of the appendicular skeleton of the holotype is a small part of a scapular blade, a nearly complete left humerus, the distal end of a right humerus, and the greater part of a right pelvis. These elements exhibit no marked differences from those of the advanced sphenacodontids *Dimetrodon* and *Sphenacodon* and they need not be described in detail here (see Romer and Price, 1940, for descriptions and illustrations). The left humerus (Fig. 3) lacks mainly the supinator process and the posterodistal margin of the entepicondyle. It has undergone some dorsoventral crushing, but still retains a slight twisting of the proximal and distal planes. The rugosities and muscle scars are well developed, suggesting a fully adult individual. As preserved, the humerus is 142.7 mm long, 69 mm wide across the proximal end, 62.1 mm across the distal end, and has a minimum dorsoventral thickness through the narrowest portion of the shaft of 11.3 mm. Important areas missing in the right pelvis (Fig. 3) include the posterior extension of the dorsal blade of the ilium, a very small amount of bone along the posterior end of the ischium, and that part of the pubis contributing to the puboischiadic plate. As preserved the ilium is 82.5 mm high, 42.4 mm across the neck, and 58.5 mm across the base, the pubis is 101 mm long, and the ischium is 80 mm in length and height. In overall proportions the only noteworthy difference I can detect between the pelvis of MCZ 3386 and those of most sphenacodontids is the relatively shorter length of its ischium compared to that of the pubis. This is true, even if one takes into account that a very small amount of bone is missing along the posterior margin of the ischium. In advanced sphenacodontids the length of the ischium normally exceeds that of the pubis by about 10%; the reverse appears to be the case in MCZ 3386.

COMPARISONS

Generic assignment of MCZ 3386 to *Ctenospondylus* is based solely on the shape and length of the neural spine of its dorsal vertebrae. In the absence of this structure it would be almost impossible to determine whether MCZ 3386 pertains to *Ctenospondylus*, *Sphenacodon*, or *Dimetrodon*, because their skeletons are otherwise essentially identical. Though Vaughn (1964, 1970) has recently found some additional differences in detail of the dermal skull roof, braincase, and the atlas-axis complex of these three genera, the neural spines remain as the major feature for distinguishing them. In *Dimetrodon* the spines are of the normal, laterally flattened shape for only a short distance above the neural arch, then abruptly change to slender, transversely expanded rods having fore and aft grooves that give them a figure-8 shape in



cross-section. These spines supported a very high sail-like structure, which in terms of the orthometric linear units of Romer and Price (1940:8)—one linear unit is defined as equal to the radius of the centrum to the $\frac{2}{3}$ power—reached a maximum length in various *Dimetrodon* species of from 90 to 156 units. In *Sphenacodon* and *Ctenospondylus* the neural spines are flat from side to side for their entire length and are also elongated, but far less so than in *Dimetrodon*. It is the degree of spine elongation that distinguishes *Sphenacodon* from *Ctenospondylus*; in the only two described North American species of the former, dorsal spine length ranges from about 14 to about 20 units, whereas in *C. casei* it has been calculated at approximately 40 units (Romer and Price, 1940) and slightly greater (Vaughn, 1964). Spine length in the only complete dorsal of *C. ninevehensis*, believed to be an anterior dorsal, is about 32 units (Table 1) and is, therefore, intermediate in length between those of *Sphenacodon* and *C. casei*.

In using spine length as a diagnostic feature in pelycosaurs it is necessary to take into account two important and closely related evolutionary trends seen in many of the better known genera—1) progressive increase in body size, and 2) disproportionate increase in spine length with increase in overall body size. Considering these trends, the greater spine length of *C. ninevehensis* over that of *Sphenacodon* is even more impressive if the comparison is limited to a species of the latter of comparable overall size. The only *Sphenacodon* species that are based on essentially complete skeletons are *S. ferox* and *S. ferocior* of North America (the Lower Permian species *Oxyodon britannicus* Huene, based on a maxilla from England, has been reassigned to *Sphenacodon* by Paton [1974] and represents the only other recognized member of this genus); both species are known from the Lower Permian of the Four Corners region of southwestern United States, and the considerably smaller *S. ferox* occurs at a somewhat lower horizon than *S. ferocior* (Romer, 1960; Vaughn, 1964). Most important, however, in *Sphenacodon*, as well as in *Dimetrodon*, there is a disproportionate increase in spine length with the increase of other linear measurements (Romer, 1948) and as noted by Romer and Price (1940), though *S. ferocior* is about 20% larger than *S. ferox* in size, it exhibits an increase in spine length of about 45%. The sizes of the centra and cranial elements, particularly the maxilla, of *C. ninevehensis* indicates an overall size well within the size range of *S. ferox*,

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Fig. 3.—*Ctenospondylus ninevehensis*, holotype, MCZ 3386. A, lateral, and B, medial views of right pelvis. C, dorsal, and D, ventral views of left humerus.

yet the dorsal spine length in the former is over 30 units, as compared to only about 14 units in the latter.

Judging from the data in Table 1, disproportionate increase in neural spine length with increase in overall size is not obvious in *Ctenospondylus*. Specimens of *C. casei* have been collected from the Lower Permian in two widely separated areas; the holotype AMNH 4047, based on a few vertebrae and rib fragments, is from north-central Texas (Romer, 1936), whereas several specimens referable to this species, including a skull and the characteristic vertebrae, have been described (Vaughn, 1964) from southeastern Utah. As noted by Vaughn (1964), though the dimensions of the one nearly complete, isolated dorsal vertebra from the Utah materials, NTM VP 1014, are considerably smaller than those of the complete dorsal of the Texas specimen, in terms of orthometric linear units (Table 1) their neural spines are very close in relative length. Because the Utah and Texas specimens are indistinguishable morphologically, so few in number, and are from deposits of equivalent age, Vaughn (1964) felt it best to refer the Utah specimens to *C. casei*, though he was aware that their difference in size and wide separation geographically raises the possibility that they may represent different species. In light of the tendency for disproportionate spine growth with increase in overall size in many pelycosaurs, the nearly equal relative lengths of the spines in the Utah and Texas forms could be viewed as indicating that their difference in overall size merely reflects a difference in growth stages of a single species. Whether or not the Utah *C. casei* represents a subadult stage of growth, it is significant that, although its overall size was probably only a little greater than that of *C. ninevehensis*, its neural spines are about 8 units longer. This comparison, however, is based on what is believed to be an anterior dorsal vertebra of *C. ninevehensis*, and had it been possible to use a vertebra of more average dimensions for the presacral column, such as a mid-dorsal, this difference may not have been as great. For instance, a relatively longer neural spine is suggested by the one mid-dorsal centrum identified in the holotype of *C. ninevehensis*. In contrast to the anterior dorsal centrum used to calculate relative spine length in the Dunkard species, the width of this centrum is less, giving a slightly smaller orthometric linear unit value, and its missing spine was probably at least a little longer, assuming that the spines reached a maximum length toward the middle of the presacral column. It is possible that the spines in *C. ninevehensis* may have reached about 35 units in length.

On the basis of relatively shorter neural spines and possibly smaller overall size the Dunkard *Ctenospondylus* can be considered not only a distinct species, but more primitive than *C. casei*. This conclusion is reinforced by differences in other features, particularly their denti-

tions. Because the sphenacodontines exhibit a general trend toward reduction of the marginal dentitions of the upper and lower jaws, the exceptionally large number of teeth in *C. ninevehensis* as compared with *C. casei* (Vaughn, 1970), which has a typical complement of marginal teeth, can be taken to mean that the former is not only more primitive than the latter, but also occupies a very primitive position within the Sphenacodontinae. The four premaxillary, 21 maxillary and the estimated 31 dentary teeth in *C. ninevehensis* represent counts equal to, or just under, the largest of those recorded for any of the sphenacodontines (see Romer and Price, 1940:Table 2). In contrast, the reconstructed skull roof of *C. casei* by Vaughn (1970) shows three premaxillary and 14 maxillary teeth with gaps for possibly two more; information on the lower jaw dentition was not given. Among the sphenacodontines presence of three premaxillary incisors is the general rule, but in some the number has been reduced to two, and only in the very small and primitive *Dimetrodon natalis* are there four. Similarly, the presence of three well-developed precanines in *C. ninevehensis* can be considered primitive; in the sphenacodontines three precanines are rare, two or one being typical, and in some they are absent. In Vaughn's (1970) reconstruction of the skull of *C. casei* two precanines are restored, but the gap seen immediately in front of the canines could have held a third precanine. Of the two North American species of *Sphenacodon*, the smaller, somewhat more primitive, *S. ferox* has a greater number of marginal teeth with maximum tooth counts of three premaxillary, 16+ maxillary, two of which are precanines, and 24 dentary teeth; *S. ferocior* shows a more advanced condition in having three premaxillary, 14 maxillary with loss of all the precanines, and approximately 21 dentary teeth. It can also be noted that, as in the skull of *C. casei*, the "step" at the anterior end of the maxilla in *C. ninevehensis* is not as pronounced as it is in *Sphenacodon* or the majority of the species of *Dimetrodon* (see Romer and Price, 1940:Figs. 4, 5).

The axial neural spine of *C. casei* is known only in the Utah materials described by Vaughn (1964) and is not only quite different from *C. ninevehensis*, but somewhat unique as revealed by his comments (1964:580) that "The posterior surface of the axial neural spine seems to have been deeply concave, but preservation is not good in this region. The posterior border of the spine meets the dorsal border at a large, semicircular notch, unlike any other sphenacodontid axis I have seen figured." Inasmuch as the axial neural spine of *C. ninevehensis* is very much like those of *Sphenacodon* and many of the species of *Dimetrodon*, such as *D. milleri* and *D. limbatus* (see Romer and Price, 1940), it seems safe to say that in this feature *C. ninevehensis* is also more primitive than *C. casei*.

DISCUSSION

Ctenospondylus ninevehensis presents the unusual situation of being considerably more primitive than *C. casei*, but occurring at an equivalent or very probably somewhat higher stratigraphic level. Vaughn (1964) correlated the vertebrate-bearing beds of the Organ Rock Shale, Cutler Group of Utah and Arizona, from which came the specimens he referred to *C. casei*, with the upper part of the Wichita Group of the Lower Permian terrestrial section of north-central Texas; the type of *C. casei* is from this part of the Texas section, the Belle Plains Formation. Following the correlations of Dunbar et al. (1960) and McKee, Oriel et al. (1967), which differ only slightly, the age of the Texas and Utah specimens of *C. casei* can be considered as earliest Leonardian. Though controversy surrounds the biostratigraphic placement of the Dunkard Group, opinions based on plants, invertebrates, and vertebrates are that it is on the whole Lower Permian (Barlow, 1975). Olson (1975) views the Dunkard vertebrate assemblage as most likely being equivalent to the Admiral and Belle Plains Formations of the Wichita Group and, thus, close to the Wolfcamp-Leonard boundary. Attempts at correlating specific horizons within the Dunkard, however, have drawn less attention. A consideration of the vertebrates from the Washington Formation, the lower of the two Dunkard formations, led Berman and Berman (1975) to conclude that they allow a range of possible correlations with the Lower Permian of Texas from about mid-Wichita up through the overlying Clear Fork Group. This in turn suggested an equivalence with either the upper part of the Wolfcampian or the base of the Leonardian Series. Using this correlation as a guide, the Nineveh Limestone, which occupies a level approximately a little more than a third of the way up through the overlying Greene Formation, can almost certainly be judged as being basal Leonard or higher. Lund (1975) has attempted to recognize vertebrate biostratigraphic zones from about mid-Allegheny Group up through the Conemaugh and Monongahela Groups to the top of the Greene Formation of the Dunkard. He presents evidence to suggest that the Greene Formation may be equivalent to the basal Leonardian lower Clear Fork beds of Texas.

Despite its late appearance, *Ctenospondylus ninevehensis* exhibits a number of characters that make it an ideal antecedent to *C. casei*—1) more primitive dentition, 2) relatively shorter neural spines, 3) more typical sphenacodontine shape of its axial neural spine, and 4) smaller overall size. At first sight it might also be suggested that *Ctenospondylus* arose from *Sphenacodon* by merely tending toward a more exaggerated growth of its neural spines, the only prominent feature that separates these two genera; in relative spine length *C. ninevehensis* is

intermediate between *S. ferocior*, the most advanced species of *Sphenacodon* in which spine length is known, and *C. casei*. There are, however, a couple of facts that argue against such a relationship. *S. ferox* and *S. ferocior* follow one another in time and are undoubtedly directly related as a species lineage that extended from a horizon considered equivalent to the Woldcampian age lower parts of the Wichita Group to one considered equivalent to the early Leonardian age basal levels of the Clear Fork Group of Texas (Langston, 1953; Romer, 1960; Vaughn, 1964). Similarly, though *C. ninevehensis* existed at about the same time or very probably somewhat later than *C. casei*, it is reasonable to assume that *C. ninevehensis*, or something very close to it, must have preceeded *C. casei* phyletically during at least early Wolfcampian time. It would, therefore, appear that *Ctenospondylus* and *Sphenacodon* were independent lineages throughout the Early Permian. Further, *C. ninevehensis* exhibits a much greater primitiveness in its dentition than *S. ferox* or *S. ferocior* and, therefore, could not have been derived from either species. It should also be mentioned here that Vaughn (1964) has shown that in features of the atlantal centrum and the braincase *Sphenacodon* and *Dimetrodon* are closer to one another than either is to *Ctenospondylus*. Needless to say, the unusual structure of the neural spines of *Dimetrodon* eliminates even the remotest possibility of it having had a direct relationship with *Ctenospondylus*. The only other Lower Permian sphenacodontine whose possible relationships to *Ctenospondylus* need be discussed here is *Neosaurus cynodus*, a small European Autunian species known only by a maxilla from the Jura region of France (Romer and Price, 1940). Its possession of the unusually high number of four precanines that are separated from a single canine by a distinct, but low, maxillary step obviously places it as a primitive member of the sphenacodontines; its 10 postcanines, however, are more characteristic of the advanced sphenacodontines and set it widely apart from *Ctenospondylus*. The few poorly known Pennsylvanian sphenacodontines also appear to be more advanced than *C. ninevehensis*. From the late Stephanian of Kounova, Czechoslovakia, have come a number of bones that have been referred to a large sphenacodontine, *Macromerion schwarzenbergii* (Romer, 1945). The holotype is a partial maxilla and, although the marginal dentition is not complete, its tooth count was certainly significantly less than that of *C. ninevehensis*. Further, through comparison with a cast of the holotype of *M. schwarzenbergii*, it is also apparent that the maxilla of *C. ninevehensis* is considerably smaller and possesses a far less prominent canine swelling, which suggests a lesser development of the canines. Vaughn (1969) has described from the Late Pennsylvanian (probably Missourian) Sangre de Cristo For-

mation of Colorado an anterior portion of a maxilla retaining two anterior teeth that probably pertains to a very small spenacodontine. Its most important diagnostic feature, as Vaughn (1969:24) points out, "is a 'step' in the maxilla such that the ventral edge of this bone anterior to the first tooth lies at a conspicuously higher level than does the rest of the ventral edge. The first tooth arises partly from the region of the step—this resembles the general condition in *Dimetrodon*." Though this specimen is much smaller than *C. ninevehensis*, it would appear that its maxillary step is more pronounced. Of the two teeth preserved in the Sangre de Cristo maxilla, undoubtedly the anterior one (6 mm long) is a precanine and the posterior one (11 mm long) a canine. Therefore, judging from Vaughn's description, it is very likely that the maxilla possessed only one, or at most two, precanines in contrast to the three seen in *C. ninevehensis*.

On what little information is available, it seems safest to assume for the present that *Ctenospondylus* became established as a distinct lineage by at least the Late Pennsylvanian and most likely arose from the haptodontine spenacodonts. It is generally accepted that the Upper Pennsylvanian-Lower Permian haptodontines of Europe and North America, represented by the genera *Haptodus* (Romer and Price, 1940; Currie, 1977) and *Cutleria* (Lewis and Vaughn, 1965), are morphologically ideal ancestors to the spenacodontines. As reasonably assumed by Currie (1977), the existence of a few poorly known or suspected spenacodontines of Late Pennsylvanian age indicates that the ancestry of the haptodontines extends back to the Early or Middle Pennsylvanian. All of the haptodontine species are very close in structure and none exhibits any features to suggest a closer affinity to *Ctenospondylus* than to any other Lower Permian spenacodontine.

It is not known whether the Dunkard *Ctenospondylus* represents a primitive holdover, as the above discussion might suggest, or whether it and the Utah and Texas representatives of this genus are members of separate lineages derived from a short-spined ancestor. In either case, the anachronistic appearance of *C. ninevehensis* lends support to the idea that some elements of the Dunkard fauna developed in isolation. Other faunal elements of the Dunkard can be cited in support of this viewpoint. The remarkable similarity between the amphibians *Diploceraspis* from the Upper Pennsylvanian and the Lower Permian Appalachian deposits and *Diplocaulus* from the Lower Permian of the southwestern United States, both noted for their bizarre "long-horned" skulls, has long been recognized (Beerbower, 1963) as a striking example of parallel evolution brought about by long-term separation. As will be reported in a future paper, a fairly good series of *Edaphosaurus* specimens is now available from throughout most of the Dunkard Group and an upper level of the underlying Monongahela

Group (considered uppermost Pennsylvanian by most). This series reveals differences from the well-documented evolutionary trends seen in the series of three consecutively occurring species of this genus, probably constituting a species phylum (Romer and Price, 1940), from the Texas Lower Permian. Although the Tri-state edaphosaur remains span a stratigraphic sequence that undoubtedly represents a considerable length of time, they do not appear to exhibit the marked increase in overall size with the time seen in the Texas species and remain within the size range of the earliest occurring Texas species, *E. boanerges*. Further, whereas in the Texas species the vertebral sail almost ceases to grow in absolute size, with later and larger species having proportionally smaller sails, those of the Tri-state edaphosaurs may increase slightly in proportion to body size with time but never attain the absolute size of the sail of *E. boanerges*. Certain of the structural trends in the neural spines of the Texas edaphosaurs, however, do seem to have been paralleled in those of the Monongahela-Dunkard edaphosaurs: 1) increased spacing and reduction in number of the tubercles of the neural spines, 2) flattening of the spine tips of the cervical vertebrae, and 3) a tendency for exuberant development of the distal-most tubercles of the spines in the cervical region.

Paleogeographic reconstructions also suggest an isolation of the Dunkard basin by the Late Pennsylvanian or the beginning of the Permian. The Dunkard basin can be thought of as a dying phase of a much larger Pennsylvanian Appalachian basin, which is typically viewed as having been a very shallow, swampy, northeastward extension of the Midcontinental seaway. It was along the eastern border of the Midcontinental seaway, which extended from Mexico to North Dakota during times of maximum advance, that the classic Lower Permian vertebrate-bearing beds of Texas and Oklahoma were deposited. It is, therefore, not unlikely that at times of maximum advance of the Appalachian arm of this seaway during the Early and Middle Pennsylvanian that an unbroken habitat zone, or zones, could have extended between the Tri-state and Midcontinental regions, providing a corridor for faunal movements. Paleogeographic reconstructions (McKee and Oriel et al., 1967) suggest, however, that with the close of the Pennsylvanian, expansion of areas of low relief may have formed a barrier, or at least a selective barrier, to faunal movements between these two regions. Unfortunately, this theory is not directly testable, because rocks of Late Pennsylvanian and Early Permian age have been removed by erosion from large parts of the central United States. The arm of the Midcontinental sea that had extended into the Appalachian geosyncline regressed southwestward by this time and any future transgressions would have probably been blocked by the further growth of existing positive areas that then completely bordered the eastern margin of the Midcontinent negative belt.

All that remained of the Appalachian basin at the onset of the Permian was the Dunkard basin. Sufficient stratigraphic and sedimentological information now exists (Arkle, 1959; Berryhill, 1967; Cross, 1975) to give a good overall picture of the physical environment of the Dunkard basin during this time. In general the Dunkard basin was a gently shelving, southwestwardly oriented, restricted basin of deposition that was bounded on the east and southeast by the active old Appalachia highlands, source of the Dunkard sediments, located on the then contiguous portions of southwestern Europe and northwestern Africa. On the west the basin was bordered by the stable continental interior, specifically the Cincinnati Arch, and separated from the Midcontinental basin complex by at least a thousand miles. With this paleogeographic setting in mind, it is easy to understand the possible occurrence of relictual or endemic forms in the Dunkard fauna.

ECOLOGY

The Nineveh Limestone undoubtedly represents a freshwater pond or lake environment. *Ctenospondylus* was a highly terrestrial and mobile genus and its preservation in this deposit was probably the result of its predation on the aquatic inhabitants of the "Nineveh" pond or lake. From the same site in which the Dunkard *Ctenospondylus* specimens were collected have also come a very large amount of remains, some partially articulated, of the amphibian *Trimerorhachis*, numerous isolated elements of the lungfish *Sagenodus*, and at least one bone, an ilium, that suggests the presence of an embolomere amphibian. Further, though the type skeleton of *C. ninevehensis* was disarticulated, its bones were preserved very close to one another and show no wear to suggest distant transport.

ACKNOWLEDGMENTS

Special acknowledgment is extended to Dr. Donald Baird of Princeton, whose keen eye discovered the site from which came not only the *Ctenospondylus* specimens described here, but other, as yet undescribed, important fossils. Further, Dr. Baird also made the first collections from this site, which included the *Ctenospondylus* specimens. Dr. James D. Beerbower of the State University of New York is also credited with having made extensive collections from this site and with having prepared many of the fossils. My appreciation is also extended to Dr. Mary Dawson, Carnegie Museum of Natural History, for critically reading the manuscript.

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PHYLOGENETIC RELATIONSHIPS OF PLESIADAPIFORM-TARSIIFORM PRIMATES

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ABSTRACT

All plesiadapiform-tarsiiform primates shared a common ancestry that involved loss of the incisors and development of the canine at the front of the jaw. Their antemolar dental complement is composed of a canine followed by five or fewer premolars. All tarsiiforms are united in having parabolic protocristae on the upper molars and include omomyines and uitasoricines (both *sensu stricto*). All plesiadapiforms have the derived protocone fold on M¹⁻². Among these, two clades are recognized—plesiadapids and paromomyids compose the Plesiadapoidea; microchoerids and anaptomorphids form the Anaptomorpoidea. Generic relationships among all plesitarsiiforms are proposed, based on inferred shared-derived similarities.

INTRODUCTION

Although the systematics and relationships of plesiadapiform-tarsiiform primates have long been the subject of intense research and spirited debate, recognition of these primates as a distinct clade occurred only recently (Gingerich, 1975, 1976). Traditionally, plesiadapiforms have included the families Plesiadapidae, Carpolestidae, Picrodontidae, and Paromomyidae and, because of their essentially Paleocene occurrence, have been accorded the status of archaic pro-

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simians (Romer, 1966; Simons, 1972). Tarsiiforms have usually been defined to include the Omomyidae, Anaptomorphidae, Tarsiidae, and Microchoeridae and portrayed as an essentially Eocene stock of primates that were morphologically intermediate between adapids, lemurs, and lorises and the higher primates, the Anthropoidea. Some authors have united the tarsiiforms and anthropoids as the Haplorhini, because extant taxa in these groups lack a moist, naked rhinarium and have fused nasal processes. In this scheme lorisiforms, lemuriforms, and adapids compose the Strepsirhini (Pocock, 1918; Hill, 1953; Martin, 1972; Szalay, 1973, 1976).

An opposing view of primate relationships recently posited by Gingerich (1975, 1976) is one with which we agree, but, as outlined below, for different reasons. Two major clades compose Primates—the Plesitarsiiformes, including all plesiadapiforms and tarsiiforms; and the Simiolemuriformes, including the strepsirhines and anthropoids.

All primates that show an absence of incisors and the development of the canine at the front of the jaw are inferred to have had a common ancestry and constitute the Plesitarsiiformes. Krishtalka (1978) suggested new relationships among the higher taxa of plesitarsiiforms. These are here explained in greater detail and to the generic level.

The dental characters cited in this study were obtained from personal examination of original and cast material of fossil plesitarsiiforms in the collections of the Section of Vertebrate Fossils, Carnegie Museum of Natural History, as well as from descriptions and illustrations in the literature. Only one conclusion is based on undescribed material.

The abbreviations in this paper are as follows: AMNH, American Museum of Natural History; CM, Carnegie Museum of Natural History; IRSNB, Institut Royal des Sciences Naturelles de Belgique; MCZ, Museum of Comparative Zoology, Harvard University; PU, Princeton University; UKMNH, University of Kansas Museum of Natural History; USNM, National Museum of Natural History (Smithsonian Institution); YPM, Yale Peabody Museum.

TARSIVS AND DENTAL HOMOLOGIES

The systematic position of *Tarsius* has been a moot point in all discussions concerning the relationships among primates. Compared with other extant primates, *Tarsius* is unique in many ways—in the adult the enormous orbits impinge on the cranium and nasal region as a result of a series of craniogenetic interactions that begin in the fetus (Starck, 1975); unlike catarrhines, in which the tubular ectotympanic extends from an extrabullar tympanic ring, the ring is intrabullar in *Tarsius* (Szalay, 1975); as far as is presently known, *Tarsius* is the only extant primate with a compound (petrosal and entotympanic) auditory bulla (Cartmill, 1975; R. D. Martin, personal communication; Schwartz [manuscript—Entotympanic contribution to the auditory bulla of *Tarsius*]; Starck, 1975; Van Kampen, 1905); although both anthropoids

and *Tarsius* have discoidal, hemochorial placentation, the processes of fetal membrane and placenta development in *Tarsius* are markedly dissimilar (Luckett, 1974, 1975; see Schwartz, 1978; Schwartz et al., 1978, for a more detailed discussion of *Tarsius*).

Dentally, *Tarsius* is especially distinct from other extant primates. Its antemolar teeth, as identified by Schwartz (1978, manuscript—Dental development, homologies, and primate phylogeny) are C^1 , $dP_1^1P_2^2dP_3^3P_4^4P_5^5$, unlike the traditional identification of $I^1I_2^2C_1^1P_2^2P_3^3P_4^4$. We think the revised dental formula of *Tarsius* reflects the true homologies of the teeth for the following reasons:

1) *Tarsius* has six upper and five lower antemolar teeth. The upper central tooth is caniniform and is followed by five premolariform teeth, of which the first and third are smallest. The five lower antemolar teeth are similarly premolariform, with the first and third smallest.

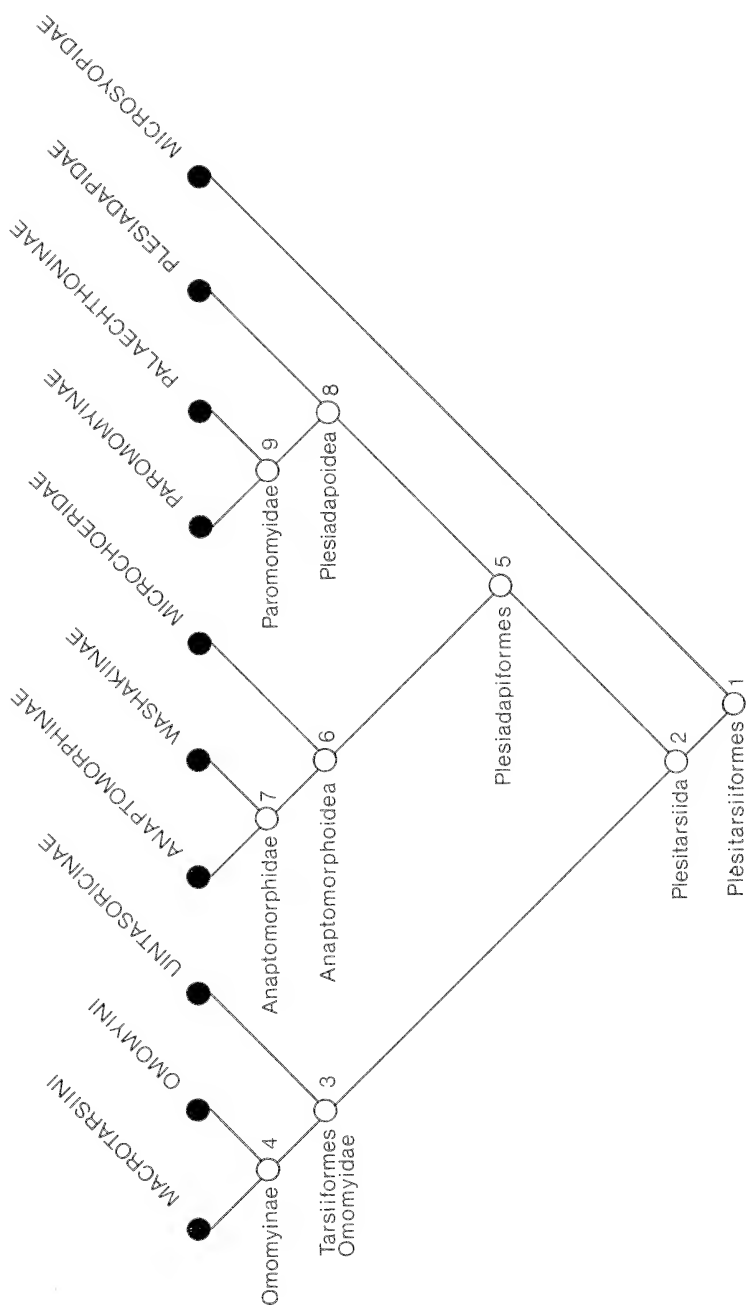
2) Comparison of sequences of dental development and eruption between *Tarsius* and other extant primates with incisiform, caniniform, and premolariform teeth in expected positions indicates that the central upper caniniform tooth of *Tarsius* develops and erupts in homologous fashion to the upper canine of these other extant primates. In the latter, the upper canine, P^2 , and P_2 develop and erupt as an integrated unit. In *Tarsius* the homologous integrated unit consists of the central upper caniniform tooth, the third upper tooth and the second lower tooth, implying that these teeth in *Tarsius* are homologous to the upper canine, P^2 , and P_2 , respectively, of extant primates.

3) If the central upper caniniform tooth in *Tarsius* is a canine, the five premolariform teeth that follow it are premolars, as are the five lower premolariform antemolar teeth. As a corollary, the third upper and second lower teeth in *Tarsius* are indeed P^2 and P_2 , respectively.

4) The small first and third premolars in *Tarsius* are not replaced and are therefore retained dP_1^1 and dP_3^3 . Thus the antemolar dental formula of *Tarsius* is properly $C^1dP_1^1P_2^2dP_3^3P_4^4P_5^5$.

5) In primates with three premolars (usually identified as $P_2^2P_3^3P_4^4$) the most frequent sequence of premolar development, eruption, and replacement is $P_2^2-P_4^4-P_3^3$. In *Tarsius* this sequence occurs as third upper tooth/second lower tooth (P_2^2)—ultimate upper and lower antemolar teeth (P_5^5)—penultimate upper and lower antemolar teeth (P_4^4). This implies that P_2^2 , P_4^4 , and P_5^5 in *Tarsius* are homologous with " $P_2^2P_3^3P_4^4$ " of three premolared primates that, according to these homologous sequences, should also be identified as P_2^2 , P_4^4 , P_5^5 . The loss of two premolars in these primates occurred at the P_1^1 and P_3^3 loci.

The occurrence of five premolars in primates is not a *de novo* event. McKenna (1975) has persuasively argued that the primitive eutherian antemolar dental complement included three incisors, a canine, and five premolars—a dental complement preserved in some specimens of



Gypsonictops and *Kennalestes*. Indeed, five premolars also seem to be retained in some erinaceids and dermopterans (Krishtalka, 1976a; Schwartz and Krishtalka, 1976), and possibly in some nyctitheriids and adapisoricids (Krishtalka, 1976a, 1976b).

These revised identifications of the premolars in *Tarsius* ($dP_1^1P_2^2dP_3^3P_4^4P_5^5$) and extant three-premolar primates ($P_2^2P_4^4P_5^5$) is cause to reevaluate the dental homologies of the antemolar teeth of other primates. Examination of plesiadapiform-tarsiiform dental remains indicates that:

1) Like *Tarsius*, all plesiadapiform-tarsiiform primates (except *Ekgmowechashala*) have a caniniform tooth at the front of the jaw followed by five or fewer premolariform teeth. When five premolariform teeth are present, the first and third are smallest. By implication, the caniniform tooth at the front of the jaw in plesiadapiform-tarsiiform primates is a canine and is followed by five premolars, of which the first and third are retained deciduous teeth.

2) The sequence of tooth replacement preserved in a partial dentary of a juvenile *Absarokius* (USNM 19198) is, as in *Tarsius* and three premolar primates: second premolariform tooth—ultimate premolariform tooth—penultimate premolariform tooth, or $P_2-P_5-P_4$. This specimen also preserves the enlarged anterior alveolus for the lower canine, a tiny alveolus for dP_1 and possibly, a small alveolus for dP_3 .

3) As discussed above in point one, in those plesiadapiform-tarsi-

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Fig. 1.—Hypothesized relationships among the major groups of plesiadapiform-tarsiiform primates (Plesitarsiiformes, Gingerich, 1976). *Node 1*—incisors lost; canine develops and erupts at the front of the jaw and is followed by five premolars of which P_1^1 and P_3^3 may be inhibited, with retention of dP_1^1 and dP_3^3 . *Node 2*—paraconid and metaconid smaller on M_{2-3} than on M_1 ; talonid cusps, especially the hypoconulid, reduced on the lower molars; hypocristid on M_{1-2} flexed at a point labial to the midline of the molar. *Node 3*—pre- and postprotocristae form a wide parabola on M^{1-3} enclosing a broad, shallow trigon basin; conules reduced; cingula on M^{1-2} extend around lingual face of the protocone; cristid obliqua on P_5M_1 are buccal to the midline of the tooth; hypoflexid notch shallow; entoconid and hypoconid flattened. *Node 4*—low, weak, lingual ridge connects distinct and well-separated paraconid and metaconid on M_{1-3} . *Node 5*—protocone fold on M^{1-2} continuous with postcingulum and enclosing posterointernal basin; M^{1-2} squared lingually, with longer lingual slope on protocone; trigonid on M_{2-3} compressed. *Node 6*—post-protocrista on M^{1-3} weaker and shorter and does not reach apex of protocone. *Node 7*— M^{1-2} more transverse; protocone with longer lingual slope and some distention of the lingual base; cristid obliqua on M_1 joins metaconid. *Node 8*—upper canine cuspsate; P_2 reduced; metacone and paraconule occur on P^5 ; metacone occurs on P^4 ; paraconid reduced on P_5M_{1-3} ; trigonid quadrate on M_1 , anteroposteriorly compressed on M_{2-3} ; M_3 with prominent third lobe and double or large hypoconulid. *Node 9*—rudimentary protocone on P^4 ; less robust lower canine; trigonid on M_{1-3} inclined anteriorly.

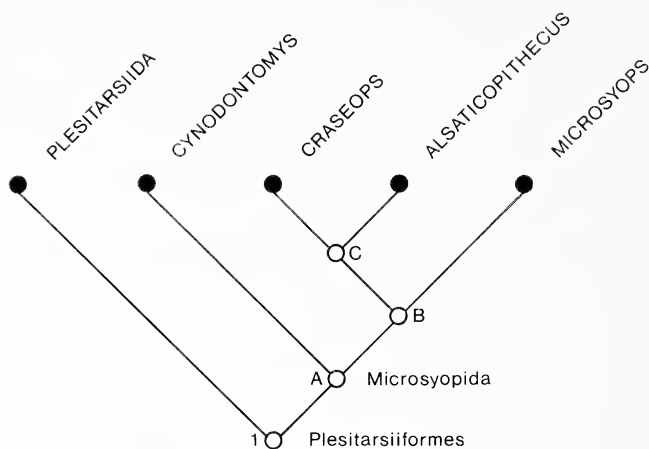


Fig. 2—Suggested relationships among microsyopids. *Node 1*—corresponds to node 1 of Fig. 1. *Node A*—proximal entoconid and hypoconid separated by a deep notch on M_{1-3} ; mesoconid on M_{1-3} ; subrescendent paracone and metacone on M^{1-2} . *Node B*—reduced, shelf-like paraconid on M_3 ; mesostyle and hypocone on M^{1-2} ; P_5 more molariform. *Node C*—sloping paraconid shelf on M_{1-3} .

iform primates with five premolars, the first and third are smallest. Sequentially, the size of the five premolars from dP_1^1 to P_5^5 is small (dP_1^1), large (P_2^2), smallest (dP_3^3), large (P_4^4), largest (P_5^5). In plesiadapiform-tarsiiform primates with fewer than five premolars, the loci of premolar loss may then be inferred from the comparative size of the remaining premolars. As expected, the most frequent sites of premolar loss appear to be the first and third—loci at which inhibition of the premanent premolars has already occurred in *Tarsius*, *Absarokius*, and, by implication, all plesiadapiform-tarsiiform primates with five premolars.

RELATIONSHIPS

Plesitarsiiformes: Microsyopids and Plesitarsiida

According to our reconstructions of dental homologies (Schwartz and Krishtalka, 1976, 1977; Schwartz, 1978, manuscript) all plesitarsiiform primates (Fig. 1, node 1) have an antemolar dental formula of a canine followed by five (possibly $dP_1^1P_2^2dP_3^3P_4^4P_5^5$) or fewer premolars. The absence of incisors, occurrence of the canine at the front of the jaw and retention of deciduous P_1^1 and P_3^3 are inferred shared-derived similarities of these primates that imply their common ancestry. Gingerich (1975, 1976) arrived at a similar conclusion also on the

basis of the morphology of the antemolar teeth, although he identified these as the traditional incisors, canine and four premolars.

If Schwartz's (manuscript) analysis of the dental homologies is correct, the origin of the plesitarsiiform primates involved loss of the incisors, development of the canine at the front of the jaw and, possibly, inhibition of permanent P_1^1 and P_3^3 . In contrast, origin of the simiolemuriforms (Gingerich, 1976) apparently involved loss of one of the five premolars (P_3^3).

The initial group to differentiate among the plesitarsiiforms were the microsyopids (Figs. 1, 2). They retain such primitive characters as a large hypoconulid, deep hypoflexid notch, and (initially) a large paraconid on the lower molars. If the entotympanic bulla of *Microsyops* (McKenna, 1966) characterizes all microsyopids, it may be a retention from the primitive primate condition or may be derived from an ancestral compound bulla. Also possibly retained is a medial entocarotid artery (McKenna, 1966; Szalay, 1969a). All microsyopids are united (Fig. 2, node A) by possession of a deep notch between the proximal hypoconulid and entoconid on the lower molars, and subcrescentic paracone and metacone on M_1^{1-3} . In *Microsyops*, *Craseops*, and *Alsaticopithecus* (Fig. 2, node B) M_1^{1-2} bear a hypocone and a mesostyle, and the paraconid on M_3 is reduced to a shelf-like crest. *Craseops* and *Alsaticopithecus* (Fig. 2, node C) are further derived in that the paraconid on M_{1-2} is also reduced to a ventrolingually sloping shelf.

All other plesitarsiiforms, the Plesitarsiida (Fig. 1, node 2), are united by a number of derived similarities—the paraconid and metaconid are smaller on M_{2-3} than on M_1 ; the talonid cusps, especially the hypoconulid, are reduced on the lower molars; on M_{1-2} the hypocristid (the crest forming the posterior rim of the talonid basin) is flexed at a point that is labial to the midline of the crown, closer to the hypoconid; the lower canine is less trenchant than at node 1. The morphology of the skulls known in a few plesitarsiid genera (*Tetonius*, *Necrolemur*, *Tarsius*, *Plesiadapis*, *Phenacolemur*) suggests that loss of the medial entocarotid artery and development of an intrabullar ectotympanic with an extrabullar tubular extension may also be derived features of this group.

Plesitarsiida: Tarsiiformes and Plesiadapiformes

Within the Plesitarsiida, two major clades are discernible, especially with regard to derived structures on the upper molars. In some plesitarsiids (Fig. 1, node 3) the pre- and postprotocristae on the upper molars form a wide, continuous parabola enclosing a broad, shallow trigon basin. Additionally, the conules are reduced, the cingula extend around part of the lingual face of the protocone, the cristid obliqua on P_5 – M_1 originates more labially so that the hypoflexid notch is shallow,

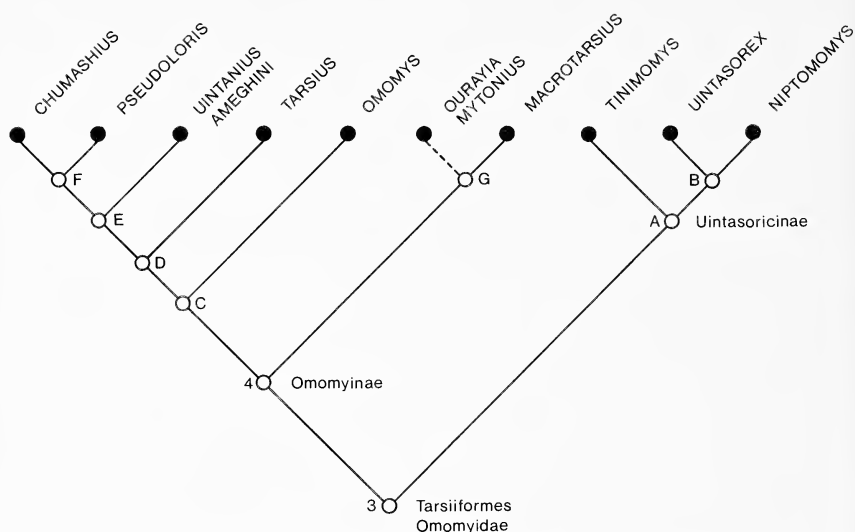


Fig. 3.—Hypothesized relationships among tarsiiforms. *Node 3*—corresponds to node 3 of Fig. 1. *Node 4*—corresponds to node 4 of Fig. 1. *Node A*—enlarged P_5^5 ; loss of premolars at P_1 and P_3 loci. *Node B*—upper molars less transverse; M_{2-3} trigonid compressed anteroposteriorly and paraconid lost; severe reduction of molar cusps. *Node C*—paraconid on M_{2-3} more medial than on M_1 . *Node D*—paraconid more medial on M_1 . *Node E*—paraconid more medial and reduced on M_{1-3} . *Node F*—paraconid closer to protoconid on M_{1-3} . *Node G*— M_{1-2} with buccal contour not emarginate, broader talonid and more lingual cristid obliqua; lower molars quadrate.

and the entoconid and hypoconid on the lower molars are flattened. This suite of derived similarities is unique to the genera in Fig. 3, here referred to the clade Tarsiiformes.

In contrast, on M^{1-2} of all other plesitarsiids (Fig. 1, node 5) the pre- and postprotocristae remain short and V-shaped, but a new crest, the protocone fold, is developed on the posterior face of the protocone. M^{1-2} are squared lingually, the protocone leans labially and has a longer lingual slope and the trigonid on M_{2-3} is anteroposteriorly compressed. Thus, all plesitarsiiform taxa with a protocone fold are regarded to have shared a common ancestry and are referred to the Plesiadapiformes, cladistically a sister group of the Tarsiiformes.

Tarsiiformes: Omomyidae (Omomyinae and Uintasoricinae)

All genera in Fig. 3 are united by the derived tarsiiform dental morphology outlined above. Among these, *Tinimomys*, *Niptomomys*, and *Uintasorex* (Fig. 3, node A) are unique in that P_5^5 are enlarged and two premolars have been lost, apparently at the P_1 and P_3 loci. These three

genera compose the Uintasoricinae (also see Krishtalka, 1978, for formal diagnosis). In *Uintasorex* and *Niptomomys* (Fig. 3, node B) the upper molars are less transverse, the trigonid on M_{2-3} is highly compressed and lacks a paraconid, and the molar cusps are reduced.

Remaining tarsiiforms (Figs. 1, 3; node 4) have a weak lingual ridge of enamel joining distinct and well-separated paraconid and metaconid on M_{1-3} . As such these genera compose the Omomyinae. A morphocline among one group of omomyines, the Omomyini (Fig. 3, nodes C, D, E, F), involves progressive reduction and more medial occurrence of the paraconid on M_{1-3} . In *Omomys* this occurs only on M_{2-3} , whereas in *Tarsius*, *Uintanius*, *Chumashius*, and *Pseudoloris* it involves M_1 and increases in degree on M_{2-3} . Thus, on M_{1-3} of *Pseudoloris* the paraconid is tiny, anteromedial and closer to the protoconid than the metaconid. *Ourayia*, *Mytonius*, and *Macrotarsius* (Krishtalka, 1978) compose the Macrotarsiini and have more nearly quadrate lower molars, much broader talonids on M_{1-2} , more buccal cristid obliquas and virtually no buccal emargination of the crown between the trigonid and talonid. Unlike the condition in the Omomyini, the paraconid on the lower molars of *Ourayia*, *Macrotarsius*, and *Mytonius* remains in its primitive lingual position.

Tinimomys.—Szalay (1974) identified *Tinimomys* as a paromomyid and Bown and Rose (1976) allocated the genus to the Microsyopidae, *incertae sedis*. The dental remains include a partial maxilla with three teeth described as P^5 – M^2 . The alleged P^5 is larger than M^1 or M^2 and is molariform in that it bears well-developed paracone, metacone, paraconule, metaconule, protocristae, continuous cingula, and pericone swelling. Such a degree of molarization commonly characterizes a deciduous ultimate premolar and this tooth may be a dP^5 . Permanent P^5 was also probably larger than M^{1-2} , but more premolariform, as is the morphology of P_5 in relation to M_{1-2} in *Tinimomys*.

Pseudoloris.—In *Pseudoloris*, usually identified as a microchoerid, the upper molars lack the protocone fold of *Nannopithex*, *Necrolemur*, *Microchoerus*, and plesiadapiforms in general. Rather, with parabolic protocristae on M^{1-3} , *Pseudoloris* is a tarsiiform and most closely related to known omomyines.

Ourayia.—The systematics of *Ourayia* have been reviewed and revised elsewhere (Krishtalka, 1978). The associated palate and partial dentaries (PU 16431) previously identified as *Ourayia* (Simons, 1961a; Szalay, 1976) and *Hemiacodon* (Robinson, 1968) are indistinguishable from *Macrotarsius*. The hypodigm of *Ourayia* is limited to the remains of the lower dentition (AMNH 1899, 1900, PU 11236, CM 12309) from the Uintan of Utah. Also *pace* Szalay (1976) *Mytonius* (Robinson, 1968) appears to be generically distinct from *Ourayia* (Krishtalka, 1978).

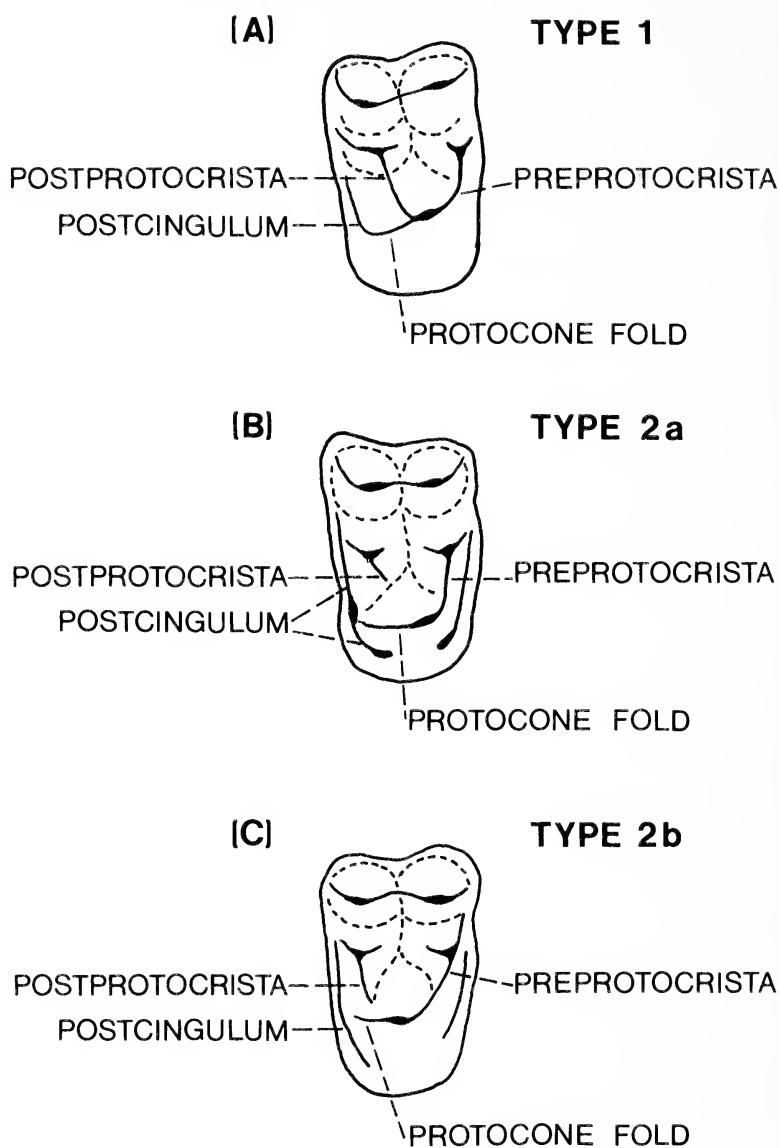


Fig. 4.—Three types of protocone fold-postcingulum configurations on M^{1-2} of plesiadapiforms. (A) Type 1—protocone fold and postcingulum continuous and enclose posterointernal basin. (B) Type 2a—postcingulum extends lingually beyond protocone fold, with weak junction marked by cuspule or wear facet. (C) Type 2b—postcingulum extends lingually beyond protocone fold, with no junction.

Uintanius.—The systematics of this genus are unclear. *U. ameghini* (Matthew, 1915; Robinson, 1966; Szalay, 1976) is known from partial upper and lower dentitions that appear to belong to the same species. This is not the case with "*U. vespertinus*" (Szalay, 1976). The upper molars, with parabolic protocristae (and no protocone fold, *pace* Szalay, 1976), are omomyid-like and may be referable to *Omomys*. The lower molars, with closely appressed paraconid and metaconid on M_{2-3} , belong to an anaptomorphid.

Plesiadapiformes: Anaptomorphoidea and Plesiadapoidea

As described above, M^{1-2} in all genera placed in the plesiadapiforms (Fig. 1, node 5) are squared linguallly as a result of the development of a protocone fold. Also the protocone leans labially and the trigonid on M_{2-3} is compressed.

Two major configurations of the protocone fold-postcingulum complex occur among plesiadapiforms—(1) in some the fold is continuous with the lingual end of the postcingulum, and a posterointernal basin is formed (Fig. 4A); (2) in others the postcingulum extends linguallly beyond the protocone fold around part or all of the base of the protocone. The latter configuration is also expressed in two ways—(2a) a weak connection between the protocone fold and postcingulum is maintained (Fig. 4B), or (2b) the protocone fold is short and does not reach the postcingulum (Fig. 4C).

Apart from the protocone fold, some plesiadapiform genera share a suite of derived features (Fig. 1, node 8) as follows: the upper canine is cuspate; P^5 bears a metacone and paraconule and a metacone occurs on P^4 ; the paraconid is reduced on P_5M_{1-3} ; the trigonid on M_1 is quadrate because the paracristid extends anteriorly from the protoconid, bends linguallly, and runs to the paraconid; in contrast, the trigonid on M_{2-3} is highly compressed anteroposteriorly and rectangular so that the paracristid and protocristid are essentially parallel; M_3 bears a prominent third lobe with a broad or double hypoconulid; P_2 is reduced. Possession of these similarities implies a common ancestry for plesiadapids (including carpolestines) and paromomyids—a relationship long recognized by other workers (Simpson, 1937, 1955; Van Valen, 1969; Rose, 1975; Simons, 1972; Gingerich, 1976) and expressed taxonomically by the clade Plesiadapoidea. All plesiadapoids have a type 1 configuration of the protocone fold-postcingulum complex (Fig. 4A)—the protocone fold is continuous with the lingual end of the postcingulum and encloses a posterointernal basin.

All other plesiadapiform genera (Fig. 1, node 6) lack these plesiadapoid features, but have a short, weak postprotocrista on M^{1-3} compared to the two other protocone crests, the preprotocrista and the protocone fold. These genera are united in the Anaptomorphoidea and

exhibit types 1, 2a and 2b configurations of the protocone fold-postcingulum complex on M^{1-2} (Fig. 4 A-C). It appears that a continuous protocone fold-postcingulum enclosing a posterointernal talon is the primitive configuration in plesiadapiforms (Fig. 1, node 5) and is retained in all plesiadapoids and some anaptomorphoids.

Anaptomorphoidea: Microchoeridae and Anaptomorphidae

All anaptomorphoids are plesiadapiforms that have a weak, short postprotocrista. Among these two clades seem discernible. The four genera referred to the Microchoeridae (Fig. 5) share a suite of derived features that is expressed as a morphocline—increasing size of the hypocone, progressive shortening of the postprotocrista, and development of more nearly square upper molars. In addition, all four genera have lost one of the five premolars, apparently from the P_3 locus. Initially in the morphocline (Fig. 5, node A) the postcingulum extends beyond the protocone fold and ends lingually in a hypocone. In *Necrolemur*, *Microchoerus*, and *Rooneyia* (Fig. 5, node B) P^5M^{1-3} are more nearly square and the hypocone is a broad-based columnar cusp that is nearly as high as the protocone and occupies almost one-half of the lingual margin of the crown. As a result the protocone fold in *Microchoerus* and *Necrolemur* (Fig. 5, node C) extends posterolabially from the apex of the protocone but is interrupted by the enlarged hypocone. Additionally, the postprotocrista is reduced to an isolated cuspule between the metaconule and the protocone, and P^5M^{1-3} are square (Hürzeler, 1948). In *Rooneyia*, the hypocone on M^{1-2} is worn on the only known specimen but is highest and most columnar among microchoerids, and is connate with the equally worn protocone. As a result, the protocone fold is obliterated and, with the increase in size of the metaconule, the postprotocrista is barely discernible.

Remaining anaptomorphoids, the Anaptomorphidae (Fig. 6), are united by the following derived features (Figs. 1, 6, node 7): M^{1-2} are more transverse; the apex of the protocone is more labial and its base is lingually distended so that the lingual slope of the cusp is longer; the cristid obliqua on M_1 joins the metaconid. These genera appear to compose two clades—among washakiines (Fig. 6, node A) the postcingulum on M^{1-2} extends lingually beyond the protocone fold and, although the protocone fold meets the postcingulum, this junction is weak and usually marked by a small cuspule or wear facet (type 2a; Fig. 4B). A hypocone and pericone occur in *Shoshonius*, *Washakius*, *Dyseolemur*, and *Hemiacodon* (Fig. 6, node B) lingual to the end of the postcingulum and precingulum, respectively, and the molar enamel is somewhat wrinkled. *Shoshonius*, *Washakius*, and *Dyseolemur* (Fig. 6, node D) have a lingual crease on the protocone of M^2 and the paraconid is more medial on M_{2-3} . The postprotocrista, a short ridge

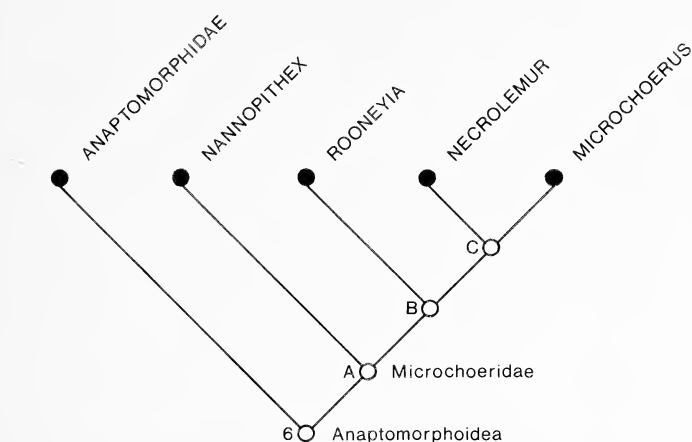


Fig. 5.—Suggested relationships among microchoerids. *Node 6*—corresponds to node 6 of Fig. 1. *Node A*—postcingulum extends lingually beyond protocone fold and ends in a hypocone; M^{1-2} more nearly quadrate; loss of one premolar (P_3); postprotocrista shorter. *Node B*—hypocone on M^{1-2} broad-based, almost as high as protocone, interrupts protocone fold; postprotocrista very short. *Node C*— M^{1-3} square; postprotocrista reduced to a cusplule between metaconule and protocone.

among these five washakiines, forms the second cusplule of the so-called “double metaconule” (Szalay, 1976) in *Washakius*.

Remaining anaptomorphids, the Anaptomorphinae (Fig. 6, node E), share a second suite of derived features— M^2 is enlarged and more transverse; the lingual slope of the protocone is much longer because the apex of the cusp occurs more labially and its base is distended linguallly; the protocone is also inflated posteriorly, so that the protocone fold is elevated; P_5 is exodaenodont buccally and higher than M_1 ; the talonid on M_{1-2} is shorter; and the paraconid and metaconid on M_{2-3} are closely appressed in marked contrast to M_1 . Unlike washakiines, neither a hypocone nor pericone occur on M^{1-2} of anaptomorphines.

Elucidation of relationships among anaptomorphines is particularly difficult because the upper dentition is unknown for *Altanius* (Dashzeveg and McKenna, 1977), *Pseudotetonius* (Bown, 1974), and *Trogolemur* (Matthew, 1909; Szalay, 1976). Also, the anterior part of the lower dentition of *Altanius* has not been recovered. Many workers are not in consensus about the hypodigm of many of these genera (see below).

Some upper molars identified as *Absarokius noctivagus* (Szalay, 1976:245, Fig. 49, AMNH 55154, 55155, YPM 17488) have a continu-

ous protocone fold-postcingulum enclosing a posterointernal talon (type 1; Fig. 4A), whereas others (Szalay, 1976:246, Fig. 50, USNM 22264) lack such a protocone fold-postcingulum continuum. Rather, as in all other described anaptomorphines, the postcingulum extends lingually beyond the protocone fold and the latter does not reach the postcingulum (type 2b; Fig. 4C). These differences warrant the exclusion of the former specimens from *Absarokius* and their inclusion in a new taxon (here dubbed "some *Absarokius*") that seems closely related to new, as yet undescribed, anaptomorphines (T. M. Bown, personal communication) that also exhibit the type 1 protocone fold-postcingulum configuration. Elements of the lower dentition identified as *A. noctivagus* may also belong to more than one genus, as is implied by the variable occurrence of a tooth at the P_3 locus among the known sample of this species. On the basis of unpublished material (T. M. Bown, personal communication), it appears that the upper molars of "*A. noctivagus*" with type 1 configuration of the protocone fold-postcingulum complex are associated with the lower jaws that lack a tooth at the P_3 locus and have a P_4 with partially fused roots. This material ("some *Absarokius*," Fig. 6) is tentatively considered most closely related to *Trogolemur* and *Pseudotetonius* (Fig. 6, node F), genera that also lack a lower premolar and have a single-rooted P_4 (Fig. 6, node G).

Among all other anaptomorphines in which M^{1-2} is known (Fig. 6, nodes H, I, K), the postcingulum extends lingually beyond the protocone fold—barely so in *Anaptomorphus* (Fig. 6, node H); more so

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Fig. 6.—Suggested relationships among anaptomorphids. *Node 6*—corresponds to node 6 of Fig. 1. *Node 7*—corresponds to node 7 of Fig. 1. *Node A*—postcingulum on M^{1-2} extends lingually beyond protocone fold; protocone fold-postcingulum junction weak and marked by weak cusplule or wear facet. *Node B*—pericone and hypocone developed at lingual end of pre- and postcingulum, respectively; molar enamel wrinkled; postproto-crista is short ridge or cusplule between metaconule and protocone. *Node C*—metastylid on M_{1-3} . *Node D*—paraconid on M_{2-3} more medial; crease on lingual face of protocone meets pericone. *Node E*— M^2 enlarged and transverse; long lingual slope on protocone due to lingual distension of base and occurrence of apex labially; protocone on M^{1-2} inflated posteriorly so that protocone fold is elevated; P_5 exodaenodont buccally and higher than M_1 ; talonid on M_{1-2} short; M_{2-3} paraconid closely appressed to metaconid in marked contrast to M_1 . *Node F*—roots of P_4 fused, at least labially; loss of one premolar. *Node G*— P_4 single-rooted. *Node H*—postcingulum extends slightly beyond protocone fold on M^{1-2} , with no junction between these two crests. *Node I*—postcingulum extends further lingually beyond protocone fold and around part of the base of the protocone. *Node J*—complete buccal cingulid on M_{1-3} . *Node K*—postcingulum extends around much of protocone; P^5 paracone and P_5 protoconid enlarged.

in *Anemorhysis* (Fig. 6, node I); and much more so in *Tetonius* and *Absarokius* (Fig. 6, node K). The latter also have a larger paracone on P⁵. *Altanius* is provisionally regarded as closely related to *Anemorhysis* (Fig. 6, node J) because both have complete buccal cingulids on the lower molars, a unique feature among anaptomorphines.

Mckennamorphus.—Szalay (1976) named *M. despairensis* from UCMP 44055, a single fragmentary dentary with part of the anterior dentition (McKenna, 1960:69) that Bown (1974) had identified as *Pseudotetonius ambiguus*. Szalay omitted any mention of *P. ambiguus*, and because UCMP 44055 does not differ from other material of this species, *Mckennamorphus* is not considered a valid taxon.

Pseudotetonius.—Of the four specimens Bown (1974) included in *P. ambiguus*, MCZ 19010, a partial left dentary with C₁, P₄₋₅M₁₋₂ and alveoli for dP₁ and P₂, differs from the other three and more closely resembles *Absarokius noctivagus* in the enlarged protoconid and buccal exodaenodonty of P₅. MCZ 19010, with a single-rooted P₄ and four premolars, is referred to "some *Absarokius*" (Fig. 6).

Chlororhysis.—Gazin (1958) identified *C. knightensis* as an omomyine from a partial dentary with P₂dP₃P₄P₅, and noted its close similarity to *Loveina*. Later (Gazin, 1962) he allocated a partial dentary with P₅M₁₋₃ to this species. Simons (1972) included *Chlororhysis* in *Tetonius* but Szalay (1976) recognized the genus as a distinct anaptomorphine. Examination of the two partial jaws indicates that, unlike anaptomorphines, the paraconid and metaconid on M₂₋₃ are not closely appressed, and the talonid on M₁₋₂ are not short. This material is not generically separable from *Loveina*.

Plesiadapioidea: Plesiadapidae and Paromomyidae

All plesiadapoids are united by a suite of derived features outlined above and in Fig. 1, node 8. These genera compose two clades—the plesiadapids (including carpolestines) (Fig. 7) and paromomyids (Fig. 8). All plesiadapids (Fig. 7, node A) lack a paraconid and talonid basin on P₅ and have a paraconule on P⁴, a margoconid on the lower canine and extremely small dP₁P₂dP₃ (Rose, 1975; Gingerich, 1976). As such, *Pronothodectes* appears to represent the ancestral condition of plesiadapines and carpolestines—a relationship also suggested by other workers (Simpson, 1937; Van Valen, 1969; Rose, 1975; Gingerich, 1976). All other plesiadapids show variable (Fig. 7, node B) or complete (Fig. 7, nodes D, E) loss of a premolar at the P₁ locus. *Elphidotarsius*, *Carpodaptus*, and *Carpolestes* (Carpolestinae, Fig. 7, node C) have long been described as a natural group and their shared-derived similarities are well known (Rose, 1975 and references therein)—P₅ is a laterally compressed trenchant blade; the trigonid on M₁ is also laterally compressed with the paraconid and metaconid more medially

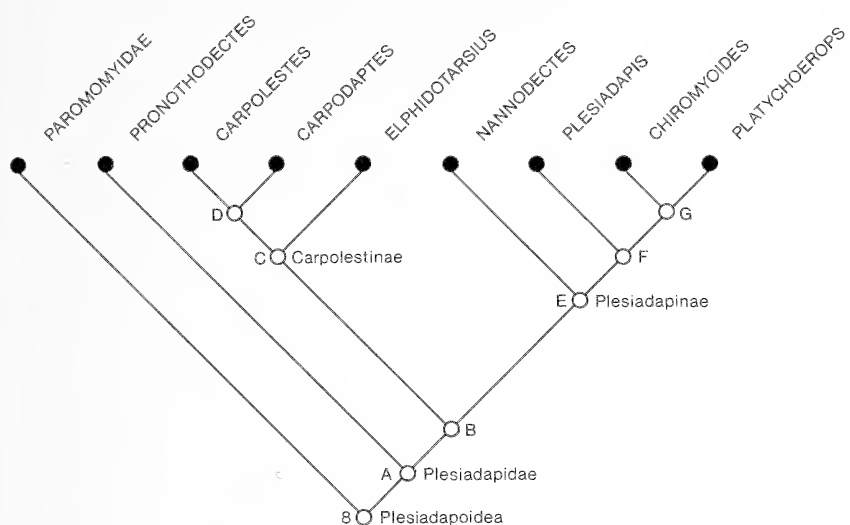


Fig. 7.—Hypothesized relationships among plesiadapids. *Node 8*—corresponds to node 8 of Fig. 1. *Node A*—paraconule on P^4 ; loss of P_5 paraconid and talonid basin; $dP_1P_2dP_3$ extremely small; margoconid on lower canine. *Node B*—variable loss of one premolar at the P_1 locus. *Node C*— P_5 is trenchant blade; M_1 laterally compressed with paraconid and metaconid more medial; P_5-M_3 exodaenodont; small hypocone on M^{1-2} . *Node D*—loss of premolars at P_1 and P_2 loci; P_4 single-rooted; P_5 enlarged with more apical cusps; M_1 paraconid directly anterior to protoconid; P^{4-5} larger than molars, polycuspidate, with three rows of cusps aligned anteroposteriorly; mandible deeper. *Node E*—loss of a premolar at P_1 locus; upper molars more quadrate, broader; lower trigonid on M_{1-3} . *Node F*—loss of second premolar (at P_2 locus); cheek teeth squared. *Node G*—loss of a third premolar (at P_3 locus).

placed; P_5-M_3 are exodaenodont; and a small hypocone occurs on M^{1-2} at the junction of the protocone fold and postcingulum. *Carpodaptes* and *Carpolestes* (Fig. 7, node D) are more derived—premolars are lost at the P_1 and P_2 loci; P_4 is single-rooted and P_5 is enlarged with more apical cusps; the paraconid on M_1 is directly anterior to the protoconid; the mandible is deeper; and P^{4-5} are larger than the molars and polycuspidate, with three anteroposterior rows of cusps.

Plesiadapines (Fig. 7, node E) parallel carpolestines in the loss of a premolar at the P_1 (*Nannodectes*) and P_2 (*Plesiadapis*, *Chiromyoides*, *Platychoerops*) loci. The upper molars are broader than in carpolestines and the trigonid on M_3 is lower. The cheek teeth are squared among more derived plesiadapines (Fig. 7, node F), and in *Platychoerops* and *Chiromyoides* (Fig. 7, node G) a third premolar is lost at the P_3 locus.

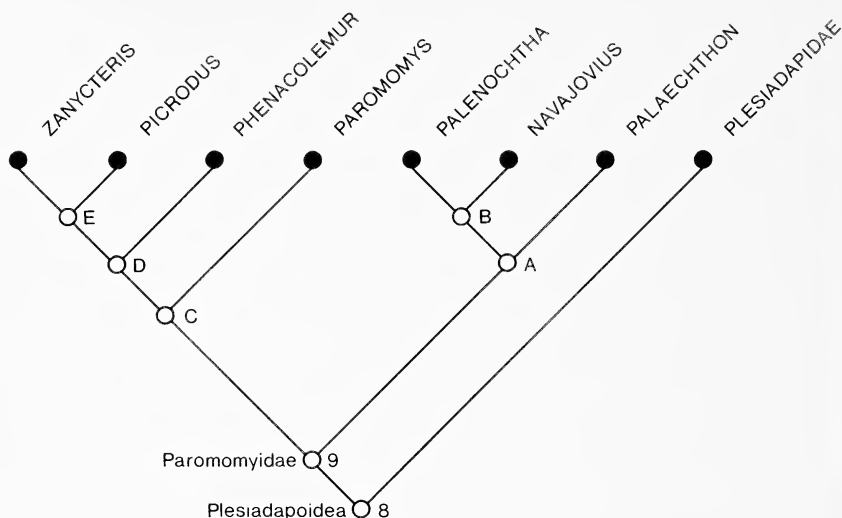


Fig. 8.—Suggested relationships among paromomyids. *Node 8*—corresponds to node 8 of Fig. 1. *Node 9*—corresponds to node 9 of Fig. 1. *Node A*—lower canine lanceolate; M_{1-3} hypoconulid closer to entoconid. *Node B*— M^3 reduced. *Node C*— M^{1-2} more nearly square, with broader and shallower talon and talonid basins, reduced cusps and conules; M_{1-3} trigonid strongly inclined anteriorly; trigonid notch reduced. *Node D*—molar cusps, crests and conules further reduced; cusps occur more marginally. *Node E*— P_5^5 enlarged; P^5 triangular, P_3 greatly elongate; M_3^3 lost; cusps, conules and crests on molars extremely reduced; metaconule marginal on M^{1-2} .

Remaining plesiadapoid genera (Figs. 1, 8, node 9) lack the shared-derived similarities of plesiadapids but are apomorphic in having a reduced P^4 with a rudimentary protocone, a less robust lower canine, and a trigonid on M_{1-3} that is inclined anteriorly. These features imply a common ancestry for the genera referred to the Paromomyidae (Fig. 8), among which two groups are commonly recognized. In *Palenochtha*, *Palaechthon* (= *Plesiolestes*, *Torrejonia*, *Talpohenach*, see below), and *Navajovius* (Fig. 8, node A) the lower canine is lanceolate (Bown and Rose, 1976), M^3 is reduced, and the hypoconulid is closer to the entoconid than the hypoconid on M_{1-3} . *Navajovius* and *Palenochtha* (Fig. 8, node B) have a more reduced M^3 .

Paromomys (= *Stockia*, see below), *Phenacolemur*, *Picrodus*, and *Zanycteris* (Fig. 8, node C) appear to compose a second group of paromomyids: M_{1-2}^{1-2} are more nearly square, with broad shallow basins, reduced cusps, and conules and a rudimentary trigonid notch on M_{1-2} . In *Phenacolemur*, *Zanycteris*, and *Picrodus* (Fig. 8, node D) the upper molars are square, the cusps occur more marginally, and the cusps, conules, and crests on the molars are further reduced, often to

no more than nubbins. In *Zanycteris* and *Picrodus* (Fig. 8, node E) these trends are expressed to a greater degree, M_3^3 are lost, P_5^5 are enlarged, and the metaconule occurs on the posterior margin of M^{1-2} (Schwartz and Krishtalka, 1977).

Palaechthon, *Torrejonia*, *Plesiolestes*, and *Talpohenach*.—Gingerich (1976, personal communication) believes that *Plesiolestes* (Jepsen, 1930) and *Palaechthon* (Gidley, 1923) are congeneric, whereas Szalay (1973) synonymized *Plesiolestes* with *Torrejonia* (Gazin, 1968, 1971), an action with which Gingerich (1976, personal communication) and Bown and Rose (1976) disagree. Kay and Cartmill (1977) named *Talpohenach* from UKMNH 7903, a partial right maxilla with $P^{3-5}M^{1-3}$ that Wilson and Szalay (1972) had identified as "an unusual variant of *Palaechthon nacimienti*." Compared with other material referred to *P. nacimienti*, UKMNH 7903 is slightly larger, P^4 has a slightly more distinct protocone, and M^{1-2} have somewhat larger styler areas. As Wilson and Szalay (1972) concluded, these differences warrant recognition of UKMNH 7903 as ?*P. nacimienti*, or perhaps as a new species of *Palaechthon*, but not generic distinction. Until material referred to these genera is restudied, *Palaechthon* is considered synonymous with *Plesiolestes*, *Torrejonia*, and *Talpohenach*.

Stockia.—*S. powayensis*, usually identified as an omomyid (Gazin, 1958; Szalay, 1976), is known only from two partial dentaries with M_{1-3} and M_{2-3} , respectively, and possibly three isolated teeth, a P_5 , dP_5 , and M_1 . Like *Paromomys*, M_{1-2} are quadrate and M_3 bears a broad third lobe with a double hypoconulid. The trigonid of M_1 is square, whereas that of M_{2-3} is a compressed rectangle with parallel protocristid and paracristid. The talonid basins are broad and shallow and the cusps are reduced, nubbins-like and marginal. These features, in part, unite paromomyines (Fig. 8, node C). *Stockia* closely resembles *Paromomys* in comparable parts of the lower dentition—a similarity also noted by McKenna (1960)—and the two are tentatively regarded as congeneric, at least until more material of "*Stockia*" is recovered. Its late Eocene occurrence parallels that of another paromomyid, *Phenacolemur* (Robinson, 1968; Krishtalka, 1978).

Elphidotarsius.—Rose (1975) described the dental formula of *Elphidotarsius* as 2.1.3.3 (or 0.1.5.3. of this paper). One of the figured partial dentaries of *E. cf. E. florencae* (Rose, 1975:14) appears to lack the alveolus for dP_1 (alveolus in front of I_2 of Rose) and its inferred dental formula is $C_1P_2dP_3P_4P_5M_{1-3}$. Loss of a premolar may be variable in *Elphidotarsius* (Fig. 7, node B).

NOVEL RELATIONSHIPS

Anaptomorphids and omomyids.—The generic composition of and allegedly close relationship between omomyids and anaptomorphids

are commonly accepted (Gazin, 1958; Simons, 1963, 1972; Szalay, 1976; Gingerich, 1976). Neither of these conclusions appear warranted if the relationships proposed above are correct. Some taxa usually identified as omomyids (*Loveina*, *Shoshonius*, *Hemiacodon*, *Dyseolemur*, *Washakius*, *Rooneyia*) have a protocone fold and V-shaped protocristae, whereas others (*Omomys*, *Chumashius*, *Macrotarsius*, *Tarsius*, *Uintanius*) lack such a fold and have widely divergent, parabolic protocristae. Possession of the protocone fold implies a common ancestry for the former genera and all others that have this derived feature and is the basis for their inclusion in the clade Plesiadapiformes. Specifically, *Rooneyia* (Wilson, 1966) is a microchoerid, and *Loveina*, *Shoshonius*, *Washakius*, *Dyseolemur*, and *Hemiacodon* are anaptomorphids (Figs. 1, 5, 6). On the other hand, possession of arcuate protocristae on the upper molars unites *Omomys*, *Chumashius*, *Macrotarsius*, *Uintanius*, *Tarsius*, *Pseudoloris*, and uintasoricines as Tarsiiformes. All anaptomorphids have the derived protocone fold and are more closely related to microchoerids, paromomyids, and plesiadapids than to tarsiiforms. Also contrary to previous conclusions (Simons, 1961b; Gingerich, 1977) *Tarsius*, a tarsiiform, and microchoerids (anaptomorphoid plesiadapiforms) do not share a descendant-ancestor relationship among plesitarsiiforms.

Microsyopids and uintasoricines.—Many workers have hypothesized a special relationship between uintasoricines and microsyopids (Szalay, 1969b) and between these groups and some paromomyids (Bown and Gingerich, 1973; Bown and Rose, 1976). Krishtalka (1978) dealt with some of the difficulties inherent in these suggestions. (1) A protocone fold and parabolic protocristae are among the derived characters for plesiadapiforms (including paromomyids) and tarsiiforms (including uintasoricines), respectively. Microsyopids are primitive in lacking a protocone fold and in having V-shaped protocristae. (2) The entoconid-hypoconulid complex does not appear to be a derived similarity in microsyopids and uintasoricines. The hypoconulid in microsyopids is large, close to the entoconid and separated from that cusp by a deep notch. In uintasoricines the hypoconulid is extremely reduced (*Uintasorex*) or often lost (*Niptomomys*, some specimens). When present, the hypoconulid is compressed anteroposteriorly to an elongate thickening of the hypocristid, of which the raised lingual end is close to the entoconid. If a notch separates the lingual end of the hypoconulid and entoconid in uintasoricines, it is extremely weak.

GENERA OMITTED

Ekgmowechashala.—Macdonald (1963, 1970) and Szalay (1976) described this Arikareean primate as an omomyid. *E. philotau* lacks the

derived antemolar morphology of plesitarsiiforms and its affinities appear to be elsewhere (Schwartz and Krishtalka, in preparation).

Teilhardina and *Purgatorius*.—Three species of *Teilhardina* have been described—the type, *T. belgica* (Simpson, 1940; Teilhard de Chardin, 1927); *T. ? gallica* (Russell et al., 1967); *T. americana* (Bown, 1976). Szalay (1976) referred *T. gallica* to a new genus, *Donrussellia*, but Savage et al. (1977) maintained that *Donrussellia* is a subgenus of *Teilhardina*. It is clear from examination of figured specimens that *T. (D.) gallica* differs significantly from the type of *T. belgica* and warrants generic distinction as *Donrussellia*, a conclusion also hinted at by Bown (1976). Moreover, Gingerich (1976, personal communication) has identified *D. gallica* as an adapid, and we concur, at least on the basis of the morphology of the lower molars.

Similarly, *T. americana* has a distinctive lower dentition compared with that of *T. belgica*— P_5M_{1-3} of *T. americana* are more robust and bear broader buccal cingulids; the talonid on M_{1-3} is broader and shorter; the paraconid and metaconid on M_{2-3} are closely appressed as in anaptomorphines; and the metaconid on M_{1-3} is not highly inflated. On the basis of the lower dentition "*T.*" *americana* appears to be an anaptomorphine plesiadapiform, and possibly a species of *Aneomorphysis* (see Bown, 1976).

The affinities of *T. belgica* are unclear. As reconstructed by Szalay (1976), and Gingerich (1977) the type specimen (IRSNB 64) appears to have two small anterior alveoli, followed by a huge alveolus for a single-rooted tooth, a much smaller alveolus, and $P_{4-5}M_{1-3}$. If these reconstructions are correct, the relative size of the alveoli implies a lower antemolar dental formula of two small incisors, a large canine, and $P_2P_4P_5$. If "alveolus a" (Gingerich, 1977) is indeed an alveolus rather than a foramen, either P_2 was double rooted, or a dP_1 was present. A second partial lower jaw of *T. belgica* (IRSNB unnumbered, Szalay, 1976:175, Fig. 2) bears a definite alveolus for a single rooted dP_1 or the anterior root of a double-rooted P_2 . Given these reconstructions, the antemolar dental formula of *T. belgica* may be, as in simi-lemuriforms, two incisors, a canine, and either three double-rooted premolars ($P_2P_4P_5$) or two single-rooted (dP_1P_2) and two double-rooted (P_4P_5) premolars. However, if the front of the jaw is reconstructed to accommodate a larger anterior tooth, such as the canine in plesitarsiiforms, the lower antemolar dental complement of *T. belgica* would be C_1 , tiny dP_1 , huge P_2 , and double-rooted P_3 (or dP_3), P_{4-5} .

The most complete described material of *Purgatorius* (Clemens, 1974) is a partial right dentary with three molars, three double-rooted premolars, and two alveoli anterior to the first premolar. The anterior end of the dentary is not preserved. Of the two alveoli, the first is

larger than the second and, as Clemens (1974) concluded, may have contained a canine followed by a single-rooted P_1 . Such a reconstruction yields an antemolar dental formula of one or more incisors (unknown), a canine, and four premolars (as in simiolemuriforms) or, if the anteriormost tooth is the canine, an antemolar dental complement ($C_1dP_1P_2P_4P_5$) found in many plesitarsiiforms. In short, the anterior dentitions of *T. belgica* and *Purgatorius* are too poorly known to confidently identify these genera as simiolemuriforms or plesitarsiiforms on that basis. The morphology of P^5-M^3 may, however, be a clue.

Elements of the upper dentition referred to *T. belgica* (Quinet, 1966a; Szalay, 1976) and *Purgatorius* (Van Valen and Sloan, 1965; Szalay, 1969a; Clemens, 1974) are closely similar. Both have an extremely weak protocone fold and a protocone that leans labially on M^{1-2} , and a metacone on P^5 —features that in part characterize plesiadapoid plesitarsiiforms (Fig. 1, nodes 5, 8). However, lower molars of *T. belgica* (Teilhard de Chardin, 1927; Quinet, 1966b; Szalay, 1976) and *Purgatorius* (Van Valen and Sloan, 1965; Szalay, 1969a; Clemens, 1974) lack the derived features of not only plesiadapoids, but primates in general. The metaconids are highly inflated and dominate the trigonid, and the talonids are not as broad as in primates. In these features the lower molars of *T. belgica* and *Purgatorius* resemble those of *Mckennatherium ladae* and "*Diacodon*" *minutus*, a primitive adapisoricid and ?condylarth, respectively (Krishtalka, 1976a). Lower molars of *T. belgica* and *Purgatorius* lack the L-shaped paracristid and quadrate trigonid on M_{1-3} of plesiadapoids, and the derived lower molar morphology of anaptomorphoids, tarsiiforms, microsypids, or adapids. The crown outlines and presence of moderately low cusps and wider talonid than trigonid on M_{1-2} may possibly imply the primate affinities of the lower molars of these genera. P_5 in both is more nearly primate-like than the molars but not unequivocally so. The talonid slope resembles that of certain adapisoricids. In summary, P_5M_{1-3} of *Purgatorius* and *T. belgica* are similar and primitive, and only their association with respective elements of their plesiadapoid-like upper dentition implies identification of these genera as primates. Many of the similarities between M^{1-2} of both taxa are also primitive—constriction across the conules; marked buccal and posterior emargination of the crown; long postmetaconulecrista and metacingulum; and strong conulecristae, postmetacrista, and metacingulum. The structure of the weak protocone fold may ally *T. belgica* and *Purgatorius* with plesiadapiforms, whereas the occurrence of a metacone on P^5 is possibly a derived feature shared with plesiadapoids. These genera are provisionally identified as primitive, closely related, plesiadapoid primates, pending a better knowledge of their anterior dentitions.

Hoangonius.—Like *Donrussellia*, Gingerich (1976) has identified *Hoangonius* as an adapid simiolemuriform.

Micromomys, *Utahia*, *Saxonella*.—These genera are too poorly known for a confident assessment of relationships (see Szalay, 1973, 1976; Rose, 1975; Bown and Rose, 1976; and references therein).

SUMMARY

The Order Primates appears to consist of two clades—the Plesitarsiiformes (including “plesiadapiforms” and “tarsiiforms”) and the Simiolemuriformes (including strepsirhines and anthropoids). Both evolved from a common ancestor that had a dental complement of two or three incisors, a canine, five premolars, and three molars. Origin of the plesitarsiiforms involved loss of the incisors, development of the canine at the front of the jaw, and, possibly, inhibition of P_1^1 and P_3^3 and retention of dP_1^1 and dP_3^3 . The ancestor of the simiolemuriforms, on the other hand, retained two incisors and the canine and had lost the premolar at the P_3^3 locus.

Apart from the microsyopids, two clades compose the Plesitarsiiformes—the Tarsiiformes, including omomyines and uitasoricines; and the Plesiadapiformes, including anaptomorphids, microchoerids, paromomyids, and plesiadapids. Each of these groups is defined by a common ancestry based on inferred shared-derived similarities, and their generic composition differs from that proposed in previous studies.

The recognition of plesitarsiiform and simiolemuriform clades implies parallel evolution of a number of features—divergent halluces and polleces, a postorbital bar, postorbital closure, a tubular ectotympanic, a petrosal bulla, nails on at least hallux and pollex, fused nasal processes, hemochorial placentation, abbreviation of the snout, and loss of the medial entocarotid artery. As suggested elsewhere (Schwartz, 1978; Schwartz et al., 1978), many of these alleged similarities between plesitarsiiforms and simiolemuriforms may be of different morphogenetic origin and not homologous. Also, some of the oft cited reconstructions of intrabullar carotid circulation for fossil and many extant primates may be erroneous (Conroy and Wible, 1978).

Some of the relationships among plesitarsiiforms proposed in this paper are novel. Determination of their validity will involve the results of new discoveries, and an aggressive frisk of the inferred shared-derived characters and alleged parallelisms.

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ARTICLE 23

REVIEW OF THE DESERT POCKET GOPHER, *GEOMYS ARENARIUS* (MAMMALIA: RODENTIA)

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ABSTRACT

The desert pocket gopher (*Geomys arenarius*), which occupies a restricted geographic range in Texas, New Mexico, and Chihuahua, was examined for morphological variation. Univariate and multivariate analyses were used to determine age, sexual, individual, and geographic variation. Significant differences were found among different age classes and between sexes. Males displayed higher individual variation than females and external measurements were more variable than cranial measurements. Two subspecies—*G. a. arenarius* and *G. a. brevirostris*—were recognized after analyses of geographic variation.

INTRODUCTION

The desert pocket gopher, *Geomys arenarius*, occupies a restricted geographic range in Texas, New Mexico, and Chihuahua, Mexico. *G. arenarius* is a member of the *bursarius*-species group as defined by Russell (1968). Alvarez (1963) seemed to suggest that *G. arenarius* was derived from *Geomys personatus* of this group, probably by invading along the Rio Grande Valley. Russell (1968) on the other hand, derived both *personatus* and *arenarius* directly from *Geomys bursarius*. Chromosomal (Davis et al., 1971), genic (Selander et al., 1975), and ectoparasite data (Price and Emerson, 1971) support the specific distinct-

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ness of *G. arenarius*. However, they do not give any conclusive answer to the relationship of *arenarius* except that it definitely belongs to the *bursarius* group.

The species was originally described by Merriam (1895) based upon specimens from El Paso, El Paso Co., Texas. The hypodigm consisted of specimens from Deming and Las Cruces, New Mexico, and Juarez, Chihuahua, as well as material from the type locality. *G. arenarius arenarius* is basically restricted to the valley of the Rio Grande, where it reaches high population levels in some areas and is considered an agricultural pest. Hall (1932) described the other currently-recognized subspecies, *G. a. brevirostris*, based upon material from the White Sands area of New Mexico.

Davis (1940) was the last person to review this species. However, with considerably more material now available, we have conducted both univariate and multivariate analyses of *Geomys arenarius*. The results of our analyses are given below.

METHODS

From all specimens, three external and 13 cranial measurements were recorded. The external measurements were as recorded by the collector; cranial measurements, as described by Williams and Genoways (1977), were taken by means of dial calipers. All measurements are given in millimeters. Specimens were assigned to one of three age groups as described by Williams and Genoways (1977).

For the analysis of geographic variation, adult specimens were grouped into nine samples as follows (Fig. 1): *sample 1*—Tularosa Basin, Otero Co., New Mexico; *sample 2*—Doña Ana Co., New Mexico, using Doña Ana, Las Cruces (except 15 mi W Las Cruces), Mesilla, Mesilla Dam, and Mesilla Park as reference points; *sample 3*—Doña Ana Co., New Mexico, specimens from 15 mi W Las Cruces and localities using Afton and Kenzin as reference points; *sample 4*—Doña Ana Co., New Mexico, and El Paso Co., Texas, using Anthony, Chamberino, and Strauss as reference points; *sample 5*—Luna Co., New Mexico, using Columbus as a reference point; *sample 6*—Chihuahua, Doña Ana Co., New Mexico, and El Paso Co., Texas, using El Paso, Fabens-Carlsbad Road, Juarez, Porvenir, and Ysleta as reference points; *sample 7*—El Paso Co., Texas, using Fabens as a reference point; *sample 8*—Chihuahua using Samalayuca as a reference point; *sample 9*—Hudspeth Co., Texas, using Fort Hancock and McNary as reference points.

Statistical procedures were performed on the IBM 370 computer at Texas Tech University. Univariate analyses were performed using the program UNIVAR. This program yields standard statistics (mean, range, standard deviations, standard error of the mean, variances, and coefficient of variation), and employs a single-classification analysis of variance (F-test, significance level 0.05) to test for significant differences between or among means (Sokal and Rohlf, 1969). When means were found to be significantly different, the Sum of Squares Simultaneous Test Procedure (SS-STP) developed by Gabriel (1964) was used to determine maximally nonsignificant subsets.

Cluster and principal components analyses were performed using the NT-SYS program. Matrices of Q-mode correlation (among OTUs) and phenetic distance coefficients were computed. Cluster analyses were conducted using UPGMA (unweighted pair-group method using arithmetic averages) on the correlation and distance matrices and a phenogram was generated for each. Phenograms were compared with their respective ma-

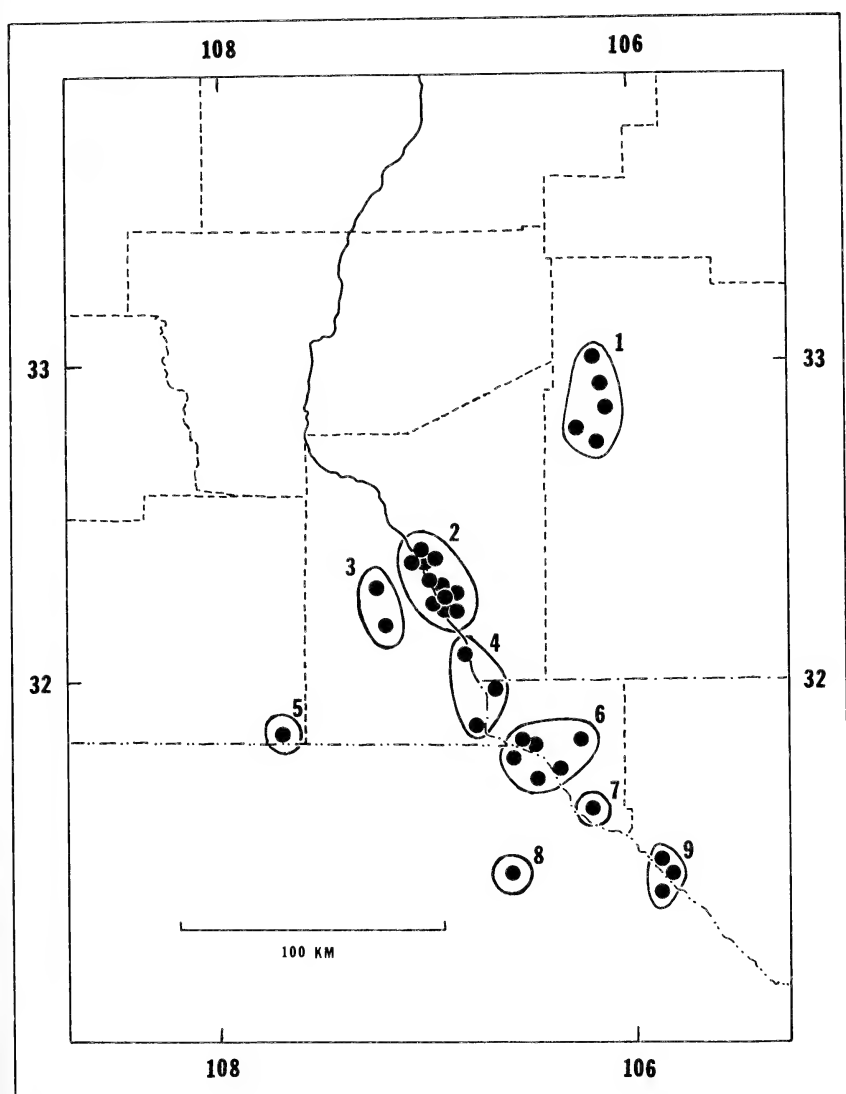


Fig. 1.—Approximate geographic areas included in the nine samples of *Geomys arenarius*. See text for localities included in each sample.

trices, and a coefficient of cophenetic correlation was computed. A matrix of Pearson's product-moment correlation among characters was computed, and the first three principal components extracted. Projections of the OTUs onto the first three principal components were made.

Discriminant function analyses were performed using the BMD-04M subroutine of the Biomedical Computer Programs (Dixon, 1971). This program used variance-covariance mathematics to weight differentially characters relative to their within-group and between-groups variation. Only two reference samples were used for all discriminant analyses in this paper. These reference samples were used to generate discriminant multipliers for each character, and these were multiplied by the value of their respective characters; all such values were summed for each individual to yield its discriminant score. Discriminant scores were obtained for individuals of questioned identity using the multipliers generated by the reference samples to obtain the identification of the questioned individuals. Specimens (40) used as a reference sample for *Geomys bursarius knoxjonesi* were as follows: NEW MEXICO: *Lea Co.*: 4.6 mi E county line, 1 (TTU). TEXAS: *Cockran Co.*: 5 mi W Morton, 1 (TTU); 1 mi W Morton, 1 (TTU); 1 mi N, 0.9 mi W Whiteface, 1 (TTU); 1 mi N, 0.5 mi W Whiteface, 1 (TTU). *Terry Co.*: 6 mi W Brownfield, 2 (TTU); 4 mi N Gomez, 5 (TTU). *Ward Co.*: 3.5 mi E Monahans, 1 (TTU). *Winkler Co.*: 4.1 mi N, 5.1 mi E Kermit, 22 (TTU); 10 mi NE Kermit, 3 (TTU); 5 mi E Kermit, 2 (TTU).

Other multivariate analyses were performed using the Statistical Analysis System (SAS) package developed by Barr and Goodnight (Service, 1972). A multivariate analysis of variance (MANOVA) and canonical analysis were performed to determine the degree of divergence among samples. Canonical analysis of the data provides weighted combinations of the characters, which maximize the distinction among groups. This analysis extracts characteristic roots and vectors and computes mean canonical variates for each sample. Additional orthogonal axes are constructed, which extract the next best combination of characters, emphasizing those with the least within-sample and greatest among-sample variation, hence, providing the next best combination of characters to discriminate among samples. Each eigenvalue and its corresponding canonical variate represents an identifiable fraction of the total variation. Both sample means and values for individuals were plotted on those canonical variates, which account for the greatest fraction of total variation. The relative importance of each original variable to a particular canonical variate was computed by multiplying the vector variable coefficient by the mean value of the dependent variable, summing all variable values for a particular vector, and then computing the percent of relative importance of each variable per vector.

RESULTS

Nongeographic Variation

The largest sample of *Geomys arenarius*, from the vicinity of Las Cruces, New Mexico, was subjected to univariate analyses to determine the type and extent of nongeographic variation in the species. We examined three types of nongeographic variation—age, secondary sexual, and individual.

Variation with age.—Table 1 gives the results of the analyses for variation with age in males and females. Fourteen of the 16 measurements studied were found to vary significantly with age in both males (length of hind foot and interorbital breadth not significant) and females (length of tail and length of hind foot not significant).

In most of the measurements tested, all three age classes recognized formed separate groups. Exceptions to these were found for total length and breadth across maxillaries for both sexes, length of tail,

Table 1.—*Variation with age in external and cranial measurements of Geomys arenarius. Age classes were tested for significant differences at the 0.05 level. Group means that were found to be significantly different were tested with SS-STP to determine the maximally nonsignificant subsets. The adult samples as listed in this table were used to test for secondary sexual variation. Measurement names marked with an asterisk indicate those with significant secondary sexual variation.*

Sex and age class	N	Mean (Range) \pm 2SE	CV	Results of SS-STP
<i>Total length*</i>				
Males				
Adults	10	261.1 (210.0–302.0) \pm 18.44	11.2	I
Subadults	28	260.3 (227.0–300.0) \pm 7.34	7.5	I
Juveniles	6	217.0 (183.0–240.0) \pm 18.83	10.6	I
Females				
Adults	22	244.8 (223.0–283.0) \pm 5.64	5.4	I
Subadults	37	239.9 (205.0–265.0) \pm 5.28	6.7	I
Juveniles	14	223.2 (166.0–250.0) \pm 10.36	8.7	I
<i>Length of tail*</i>				
Males				
Adults	9	90.7 (78.0–101.0) \pm 4.98	8.2	I
Subadults	29	86.4 (60.0–109.0) \pm 4.17	13.0	I
Juveniles	6	72.5 (58.0– 85.0) \pm 7.64	12.9	I
Females				
Juveniles	14	78.0 (47.0– 87.0) \pm 5.28	12.7	ns
Subadults	38	77.5 (50.0– 93.0) \pm 2.93	11.6	
Adults	22	76.8 (52.0– 95.0) \pm 4.14	12.7	
<i>Length of hind foot*</i>				
Males				
Subadults	29	32.9 (30.0– 35.0) \pm 0.80	6.5	ns
Adults	11	32.3 (28.0– 37.0) \pm 0.94	4.8	
Juveniles	6	31.2 (28.0– 34.0) \pm 1.82	7.2	
Females				
Subadults	38	31.1 (25.0– 36.0) \pm 0.71	7.1	ns
Adults	22	30.5 (22.0– 34.0) \pm 1.15	8.8	
Juveniles	14	29.6 (23.0– 35.0) \pm 1.60	10.1	
<i>Greatest length of skull*</i>				
Males				
Adults	11	46.0 (42.0– 49.4) \pm 1.47	5.3	I
Subadults	26	44.6 (39.1– 48.2) \pm 0.96	5.5	I
Juveniles	6	37.3 (32.8– 39.6) \pm 2.09	6.9	I
Females				
Adults	23	42.9 (41.1– 45.9) \pm 0.47	2.6	I
Subadults	32	41.5 (37.9– 44.5) \pm 0.62	4.2	I
Juveniles	13	38.0 (36.1– 42.0) \pm 0.93	4.4	I

Table 1.—(Continued)

Sex and age class	N	Mean (Range) \pm 2SE	CV	Results of SS-STP
<i>Condylbasal length*</i>				
Males				
Adults	13	45.1 (40.8– 48.8) \pm 1.30	5.2	I
Subadults	31	42.8 (37.7– 46.7) \pm 0.99	6.4	I
Juveniles	6	36.2 (31.8– 38.8) \pm 2.04	6.9	I
Females				
Adults	22	41.7 (39.3– 44.3) \pm 0.50	2.8	I
Subadults	38	40.4 (36.9– 44.1) \pm 0.57	4.3	I
Juveniles	14	36.3 (29.2– 40.5) \pm 1.36	7.0	I
<i>Basal length*</i>				
Males				
Adults	13	42.6 (38.2– 46.4) \pm 1.33	5.6	I
Subadults	31	40.0 (35.0– 43.9) \pm 0.94	6.5	I
Juveniles	6	33.2 (29.0– 35.7) \pm 2.01	7.4	I
Females				
Adults	22	39.2 (36.8– 41.8) \pm 0.50	3.0	I
Subadults	38	37.7 (34.4– 40.6) \pm 0.55	4.5	I
Juveniles	14	33.7 (26.6– 38.1) \pm 1.37	7.6	I
<i>Palatal length*</i>				
Males				
Adults	13	29.3 (25.9– 33.2) \pm 1.10	6.8	I
Subadults	31	27.4 (23.6– 30.3) \pm 0.74	7.5	I
Juveniles	6	22.2 (19.1– 24.3) \pm 1.52	8.4	I
Females				
Adults	23	26.9 (25.1– 28.7) \pm 0.37	3.3	I
Subadults	38	25.6 (22.9– 28.2) \pm 0.42	5.0	I
Juveniles	14	22.6 (17.4– 25.8) \pm 1.02	8.4	I
<i>Palatofrontal depth*</i>				
Males				
Adults	13	16.6 (14.7– 18.1) \pm 0.54	5.8	I
Subadults	31	15.9 (13.9– 17.5) \pm 0.36	6.3	I
Juveniles	6	13.4 (12.0– 14.7) \pm 0.74	6.8	I
Females				
Adults	24	15.8 (14.6– 17.1) \pm 0.22	3.5	I
Subadults	39	15.1 (13.5– 16.7) \pm 0.23	4.8	I
Juveniles	14	13.5 (11.5– 15.1) \pm 0.45	6.3	I
<i>Length of nasals*</i>				
Males				
Adults	11	16.7 (14.4– 18.9) \pm 0.86	8.5	I
Subadults	26	15.8 (13.2– 18.7) \pm 0.55	8.9	I
Juveniles	6	12.8 (11.3– 13.9) \pm 0.78	7.4	I

Table 1.—(Continued)

Sex and age class	N	Mean (Range) \pm 2SE	CV	Results of SS-STP
Females				
Adults	23	15.1 (12.9– 16.9) \pm 0.34	5.3	I
Subadults	32	14.4 (12.4– 15.9) \pm 0.36	7.0	I
Juveniles	13	12.9 (11.8– 15.2) \pm 0.50	7.0	I
<i>Diastema*</i>				
Males				
Adults	13	15.7 (12.8– 18.7) \pm 0.80	9.1	I
Subadults	32	14.3 (11.6– 16.1) \pm 0.47	9.4	I
Juveniles	6	10.8 (8.8– 12.1) \pm 0.92	10.5	I
Females				
Adults	24	14.0 (12.5– 14.9) \pm 0.26	4.5	I
Subadults	39	13.1 (11.5– 15.1) \pm 0.27	6.3	I
Juveniles	14	11.1 (7.8– 13.2) \pm 0.65	10.9	I
<i>Zygomatic breadth*</i>				
Males				
Adults	13	28.7 (25.1– 31.6) \pm 1.00	6.2	I
Subadults	31	26.3 (22.8– 30.3) \pm 0.74	7.8	I
Juveniles	6	20.7 (17.5– 21.9) \pm 1.36	8.1	I
Females				
Adults	23	25.9 (23.5– 28.6) \pm 0.53	4.9	I
Subadults	37	24.5 (21.0– 26.8) \pm 0.45	5.6	I
Juveniles	14	21.1 (17.1– 24.4) \pm 0.85	7.5	I
<i>Mastoid breadth*</i>				
Males				
Adults	13	25.8 (23.7– 28.6) \pm 0.80	5.6	I
Subadults	31	24.4 (21.6– 27.0) \pm 0.50	5.8	I
Juveniles	6	20.6 (17.9– 21.8) \pm 1.18	7.0	I
Females				
Adults	24	24.1 (22.4– 25.7) \pm 0.31	3.2	I
Subadults	39	22.9 (20.5– 24.5) \pm 0.31	4.2	I
Juveniles	14	20.9 (17.3– 23.5) \pm 0.78	7.0	I
<i>Squamosal breadth*</i>				
Males				
Adults	13	18.9 (18.1– 20.3) \pm 0.40	3.8	I
Subadults	31	18.8 (16.5– 19.9) \pm 0.78	5.6	I
Juveniles	6	16.7 (14.7– 17.5) \pm 0.85	6.2	I
Females				
Adults	24	18.4 (17.2– 19.5) \pm 0.28	3.7	I
Subadults	39	17.8 (16.1– 19.4) \pm 0.20	3.5	I
Juveniles	14	17.0 (15.6– 17.6) \pm 0.29	3.2	I

Table 1.—(Continued)

Sex and age class	N	Mean (Range) \pm 2SE	CV	Results of SS-STP
<i>Rostral breadth*</i>				
Males				
Adults	13	10.6 (9.7– 11.6) \pm 0.36	6.1	I
Subadults	32	10.0 (9.1– 11.4) \pm 0.21	6.0	I
Juveniles	6	8.6 (7.9– 9.3) \pm 0.43	6.1	I
Females				
Adults	24	9.9 (9.0– 10.6) \pm 0.19	4.8	I
Subadults	39	9.4 (8.5– 10.4) \pm 0.15	5.1	I
Juveniles	14	8.5 (7.2– 9.5) \pm 0.30	6.7	I
<i>Interorbital constriction</i>				
Males				
Adults	13	6.5 (5.9– 7.1) \pm 0.19	5.3	ns
Subadults	32	6.4 (5.7– 7.0) \pm 0.11	5.0	
Juveniles	6	6.3 (6.0– 6.8) \pm 0.28	5.4	
Females				
Adults	24	6.3 (5.4– 7.0) \pm 0.14	5.3	I
Subadults	39	6.3 (5.6– 7.8) \pm 0.13	6.2	I
Juveniles	14	6.0 (5.6– 6.6) \pm 0.16	5.1	I
<i>Breadth across maxillaries</i>				
Males				
Adults	13	7.9 (7.2– 8.6) \pm 0.25	5.6	I
Subadults	32	7.8 (7.0– 8.3) \pm 0.11	4.1	I
Juveniles	6	7.4 (6.7– 7.7) \pm 0.34	5.6	I
Females				
Adults	24	7.7 (7.3– 8.3) \pm 0.09	2.9	I
Subadults	39	7.5 (6.7– 8.4) \pm 0.10	4.0	I
Juveniles	14	7.2 (6.7– 7.9) \pm 0.15	4.0	I

greatest length of skull, palatofrontal depth, length of nasals, and squamosal breadth for males and interorbital breadth for females. In all of these characters, the adults and subadults formed a group differing significantly from the juveniles. Adults averaged the largest in all measurements except length of tail for females in which the juveniles were the largest, and length of hind foot for both sexes in which the subadults were largest.

Clearly, the three ages that we recognized are morphologically distinct. In the following analyses, we have used only adults.

Secondary sexual variation.—The same adult male and female samples used in the variation with age analyses were used to test for secondary sexual variation (Table 1). Males averaged significantly large-

er than females in all measurements except in interorbital constriction and breadth across maxillaries. Even in these two measurements, in which there were no significant differences, the males averaged larger than the females. In all analyses of geographic variation, males and females were treated separately.

Individual variation.—Coefficients of variation for adult males ranged from 3.8 to 11.2 and for adult females from 2.6 to 12.7 for the 16 external and cranial measurements tested (Table 1). The coefficients of variation for the external measurements are generally higher than for cranial measurements with length of hind foot for males being the exception. Squamosal breadth had the lowest value (3.8) and diastema had the highest value (9.1) for cranial measurements for males; for females, greatest length of skull had the lowest value (2.6) and length of nasals and interorbital constriction had the highest values (5.4 and 5.3, respectively). The mean coefficient of variation for the 16 measurements was 6.4 for males and 4.8 for females. Males had larger coefficients of variation than females for all measurements except interorbital constriction in which both sexes had a value of 5.3.

Geographic Variation

Univariate analyses.—Five samples of both males and females had a sufficient number of specimens to allow their use in the univariate analyses. For males, the samples were as follows: sample 1, vicinity of Whites Sands National Monument, New Mexico; sample 2, vicinity of Las Cruces, New Mexico; sample 3, vicinity of Kenzin, New Mexico; sample 6, vicinity of El Paso, Texas; sample 7, vicinity of Fabens, Texas. For females, sample 3 was replaced by sample 9 from the vicinity of Ft. Hancock, Texas. Results of the analyses of variance and SS-STP for these samples are given in Table 2.

All measurements except squamosal breadth for males and interorbital constriction for females exhibited significant geographic variation. In males, samples 1 and 3 averaged the smallest in size for all measurements except interorbital constriction, in which samples 1 and 7 averaged the smallest in size. Samples 6 and 7 averaged the largest in size for males in all measurements except rostral breadth, interorbital constriction, length of nasals, and zygomatic breadth. In the last three of these measurements, specimens from sample 6 averaged the largest in size.

The SS-STP analyses separate the samples of males into two basic groups—1 and 3, and 2, 6, and 7. Samples 1 and 3 are significantly different from the other three samples in greatest length of skull and condylobasal length. In six other measurements (basal length, palatal length, palatofrontal depth, diastema, zygomatic breadth, and mastoid breadth), two or three overlapping subsets of samples are formed, but

Table 2.—*Geographic variation in external and cranial measurements of Geomys arenarius. Samples are defined in text. Samples were tested for significant differences at the 0.05 level. Sample means that were found to be significantly different were tested with SS-STP to determine the maximally nonsignificant subsets.*

Sex and locality number	N	Mean (Range) \pm 2SE	CV	Results of SS-STP
<i>Total length</i>				
Males				
7	4	284.2 (277.0–291.0) \pm 7.86	2.8	I
6	6	280.5 (271.0–289.0) \pm 6.61	2.9	I I
2	11	261.4 (210.0–302.0) \pm 16.69	10.6	I I
1	9	253.4 (236.0–275.0) \pm 8.12	4.8	I
3	3	251.0 (237.0–260.0) \pm 14.19	4.9	I
Females				
7	15	251.7 (236.0–267.0) \pm 4.39	3.4	I
6	24	245.8 (218.0–273.0) \pm 5.03	5.0	I
2	27	243.3 (222.0–283.0) \pm 5.27	5.6	I I
9	6	234.7 (225.0–245.0) \pm 6.38	3.3	I I
1	13	233.3 (220.0–256.0) \pm 6.31	4.9	I
<i>Length of tail</i>				
Males				
7	4	97.4 (91.0–106.0) \pm 6.61	6.8	I
6	6	91.7 (82.0– 95.0) \pm 4.06	5.4	I I
2	10	90.1 (78.0–101.0) \pm 4.59	10.9	I I
1	9	83.9 (75.0– 97.0) \pm 5.42	9.7	I I
3	3	82.3 (73.0– 91.0) \pm 10.41	10.9	I
Females				
7	15	81.1 (67.0– 98.0) \pm 3.88	9.3	I
9	6	78.2 (73.0– 82.0) \pm 3.32	5.2	I I
2	27	76.7 (52.0– 95.0) \pm 3.45	11.7	I I
6	24	76.7 (61.0– 90.0) \pm 2.88	9.2	I I
1	13	71.8 (60.0– 80.0) \pm 3.85	9.7	I
<i>Length of hind foot</i>				
Males				
6	6	33.5 (31.0– 35.0) \pm 1.13	4.1	I
7	4	33.5 (32.0– 35.0) \pm 1.29	3.9	I
2	12	32.4 (30.0– 35.0) \pm 0.90	4.8	I I
1	9	31.0 (30.0– 33.0) \pm 0.71	3.4	I
3	3	30.3 (29.0– 31.0) \pm 1.33	3.8	I
Females				
6	24	31.6 (27.0– 35.0) \pm 0.71	5.5	I
9	6	31.4 (30.0– 32.0) \pm 0.75	2.9	I
7	15	30.6 (28.0– 32.0) \pm 0.55	3.4	I I
2	27	30.5 (22.0– 34.0) \pm 0.95	8.1	I I
1	13	28.8 (27.0– 31.0) \pm 0.69	4.3	I

Table 2.—(Continued)

Sex and locality number	N	Mean (Range) \pm 2SE	CV	Results of SS-STP
<i>Greatest length of skull</i>				
Males				
6	7	47.2 (45.1– 48.9) \pm 0.93	2.6	I
7	4	46.7 (45.6– 48.6) \pm 1.37	2.9	I
2	12	45.9 (42.0– 43.2) \pm 1.34	5.1	I
1	10	42.8 (40.5– 45.7) \pm 1.05	3.9	I
3	3	42.3 (41.0– 43.2) \pm 1.33	2.7	I
Females				
7	14	43.9 (41.7– 46.1) \pm 0.68	2.9	I
6	20	43.4 (40.7– 49.9) \pm 0.85	4.4	I
2	27	42.6 (39.9– 45.9) \pm 0.54	3.3	I
9	3	42.0 (41.4– 42.6) \pm 0.70	1.4	I I
1	10	38.8 (37.1– 42.8) \pm 1.15	4.7	I
<i>Condylobasal length</i>				
Males				
6	7	45.9 (44.2– 47.5) \pm 0.87	2.5	I
7	4	45.6 (43.8– 47.6) \pm 1.58	3.5	I
2	14	45.0 (40.8– 48.8) \pm 1.15	5.0	I
1	10	41.6 (39.3– 44.5) \pm 1.04	4.0	I
3	3	41.2 (40.2– 42.2) \pm 1.15	2.4	I
Females				
7	15	43.1 (41.5– 45.6) \pm 0.64	2.9	I
6	24	41.6 (39.5– 43.8) \pm 0.52	3.0	I
2	27	41.3 (38.7– 44.3) \pm 0.57	3.6	I
9	6	40.7 (40.1– 41.6) \pm 0.45	1.4	I
1	13	38.1 (35.9– 41.5) \pm 0.98	4.6	I
<i>Basal length</i>				
Males				
6	7	43.6 (42.3– 45.3) \pm 0.85	2.6	I
7	4	42.9 (41.1– 44.5) \pm 1.40	3.3	I I
2	14	42.5 (38.2– 46.4) \pm 1.24	5.5	I I
3	3	39.0 (38.0– 40.0) \pm 1.16	2.6	I I
1	10	38.9 (35.9– 41.4) \pm 1.15	4.7	I
Females				
7	15	40.9 (39.1– 42.9) \pm 0.59	2.8	I
6	24	39.0 (37.1– 41.3) \pm 0.48	3.0	I
2	27	38.8 (36.0– 41.8) \pm 0.57	3.8	I
9	6	38.1 (37.4– 38.7) \pm 0.38	1.2	I
1	13	35.5 (33.5– 38.8) \pm 0.95	4.8	I

Table 2.—(Continued)

Sex and locality number	N	Mean (Range) \pm 2SE	CV	Results of SS-STP
<i>Palatal length</i>				
Males				
6	7	30.0 (28.7– 31.7) \pm 0.90	4.0	I
7	4	29.4 (28.0– 30.3) \pm 1.00	3.4	I I
2	14	29.2 (25.9– 33.2) \pm 1.05	6.7	I I
3	3	26.5 (26.0– 27.5) \pm 0.97	3.2	I I
1	10	26.1 (23.8– 28.0) \pm 0.88	5.3	I
Females				
7	15	27.9 (26.1– 29.7) \pm 0.50	3.5	I
2	28	26.6 (23.9– 28.7) \pm 0.43	4.3	I
6	24	26.6 (25.0– 28.1) \pm 0.39	3.6	I
9	6	26.1 (25.8– 26.6) \pm 0.23	1.1	I
1	13	23.5 (21.8– 26.0) \pm 0.72	5.5	I
<i>Palatofrontal depth</i>				
Males				
6	7	17.1 (16.1– 17.7) \pm 0.50	3.9	I
7	4	16.7 (15.3– 17.7) \pm 1.08	6.5	I
2	14	16.6 (14.7– 18.1) \pm 0.50	5.7	I
3	3	15.6 (15.0– 16.1) \pm 0.66	3.6	I I
1	10	15.5 (14.9– 16.1) \pm 0.25	2.6	I
Females				
7	15	16.1 (15.3– 16.9) \pm 0.28	3.4	I
2	29	15.7 (14.6– 17.1) \pm 0.23	3.9	I I
6	25	15.5 (14.5– 16.5) \pm 0.23	3.7	I
9	6	15.2 (14.7– 15.7) \pm 0.28	2.3	I I
1	13	14.7 (14.2– 16.0) \pm 0.34	4.1	I
<i>Length of nasals</i>				
Males				
6	7	17.5 (16.7– 18.4) \pm 0.49	3.7	I
2	12	16.8 (14.4– 18.9) \pm 0.80	8.2	I I
7	4	16.6 (15.2– 17.9) \pm 1.14	6.9	I I I
3	3	14.7 (14.4– 15.1) \pm 0.44	2.6	I I
1	10	14.6 (13.3– 15.6) \pm 0.50	5.4	I
Females				
7	14	15.7 (14.6– 16.9) \pm 0.39	4.7	I
6	20	15.3 (14.0– 16.6) \pm 0.34	4.9	I
2	27	15.1 (12.9– 16.9) \pm 0.33	5.7	I
9	3	14.8 (14.4– 15.5) \pm 0.68	4.0	I
1	10	13.0 (11.6– 14.9) \pm 0.67	8.2	I

Table 2.—(Continued)

Sex and locality number	N	Mean (Range) \pm 2SE	CV	Results of SS-STP
<i>Diastema</i>				
Males				
7	4	16.1 (15.1– 16.7) \pm 0.79	4.9	I
6	7	15.9 (14.3– 17.1) \pm 0.73	6.1	I
2	14	15.6 (12.8– 18.7) \pm 0.75	8.9	I I
1	10	14.2 (12.9– 15.3) \pm 0.57	6.4	I I
3	3	13.9 (13.1– 14.6) \pm 0.87	5.4	I
Females				
7	15	15.1 (14.0– 16.0) \pm 0.32	4.2	I
6	25	13.9 (12.7– 15.0) \pm 0.26	4.6	I
2	29	13.8 (12.4– 14.9) \pm 0.28	5.5	I
9	6	13.8 (13.3– 14.2) \pm 0.30	2.7	I
1	13	12.4 (11.3– 14.2) \pm 0.56	8.1	I
<i>Zygomatic breadth</i>				
Males				
6	7	29.1 (27.1– 31.6) \pm 1.09	5.0	I
2	14	28.6 (25.1– 31.6) \pm 0.94	6.1	I
7	4	28.5 (27.6– 29.5) \pm 0.79	2.8	I
3	3	26.8 (25.9– 27.3) \pm 0.87	2.8	I I
1	10	25.6 (23.3– 27.8) \pm 0.94	5.8	I
Females				
7	15	27.0 (24.9– 28.5) \pm 0.51	3.6	I
2	28	25.6 (23.0– 28.6) \pm 0.52	5.4	I
6	25	25.3 (22.7– 29.0) \pm 0.48	4.8	I
9	6	24.6 (23.1– 25.4) \pm 0.69	3.4	I I
1	13	22.8 (20.7– 26.1) \pm 0.82	6.5	I
<i>Mastoid breadth</i>				
Males				
6	7	26.3 (24.5– 28.2) \pm 1.04	5.2	I
7	4	25.8 (24.2– 27.3) \pm 1.28	5.0	I
2	14	25.7 (23.7– 28.6) \pm 0.75	5.5	I
3	3	24.5 (23.9– 25.2) \pm 0.75	2.7	I I
1	10	24.0 (22.9– 25.6) \pm 0.57	3.8	I
Females				
7	14	24.6 (22.3– 26.1) \pm 0.47	3.6	I
2	29	23.8 (21.2– 25.7) \pm 0.36	4.0	I I
6	25	23.6 (21.6– 26.5) \pm 0.42	4.5	I I
9	6	23.2 (22.6– 23.7) \pm 0.34	1.8	I I
1	13	22.2 (20.7– 24.0) \pm 0.59	4.8	I

Table 2.—(Continued)

Sex and locality number	N	Mean (Range) \pm 2SE	CV	Results of SS-STP
<i>Squamosal breadth</i>				
Males				
6	7	19.2 (17.5– 20.3) \pm 0.75	5.2	ns
7	4	19.1 (17.4– 20.1) \pm 1.20	6.3	
2	14	18.8 (17.8– 20.3) \pm 0.41	4.0	
3	3	18.5 (17.9– 18.9) \pm 0.59	2.8	
1	10	18.4 (17.2– 19.6) \pm 0.43	3.7	
Females				
7	15	18.8 (17.4– 19.6) \pm 0.28	2.9	I
2	29	18.3 (16.8– 19.5) \pm 0.27	4.0	I I
6	25	18.0 (16.8– 19.7) \pm 0.27	3.7	I I
1	13	17.5 (16.3– 18.5) \pm 0.40	4.1	I
9	6	17.4 (17.0– 18.0) \pm 0.29	2.0	I
<i>Rostral breadth</i>				
Males				
2	14	10.6 (9.7– 11.6) \pm 0.33	5.9	I
6	7	10.4 (9.9– 11.3) \pm 0.37	4.7	I I
7	4	10.1 (9.7– 10.3) \pm 0.26	2.6	I I
3	3	9.8 (9.5– 10.1) \pm 0.35	3.1	I I
1	10	9.6 (8.9– 10.3) \pm 0.26	4.3	I
Females				
2	29	9.8 (8.7– 10.6) \pm 0.19	5.3	I
7	15	9.6 (8.6– 10.3) \pm 0.24	4.8	I
6	25	9.5 (8.7– 10.4) \pm 0.14	3.7	I
9	6	9.4 (9.6– 9.8) \pm 0.39	5.0	I I
1	13	9.0 (8.6– 9.6) \pm 0.17	3.5	I
<i>Interorbital constriction</i>				
Males				
6	7	6.6 (6.1– 7.4) \pm 0.32	6.5	I
2	14	6.5 (5.9– 7.1) \pm 0.18	5.1	I
3	3	6.4 (6.3– 6.6) \pm 0.20	2.7	I I
7	4	6.2 (5.8– 6.6) \pm 0.35	5.7	I I
1	10	6.1 (5.4– 6.5) \pm 0.19	5.0	I
Females				
2	29	6.3 (5.4– 7.0) \pm 0.12	5.2	ns
6	25	6.3 (5.8– 6.9) \pm 0.14	5.3	
9	6	6.3 (5.9– 6.9) \pm 0.28	5.4	
7	15	6.2 (5.4– 6.8) \pm 0.21	6.6	
1	13	6.1 (5.6– 6.4) \pm 0.12	3.5	

Table 2.—(Continued)

Sex and locality number	N	Mean (Range) \pm 2SE	CV	Results of SS-STP
<i>Breadth across maxillaries</i>				
Males				
6	7	8.5 (8.1– 9.0) \pm 0.24	3.8	I
7	4	7.9 (7.5– 8.1) \pm 0.26	3.3	I
2	14	7.9 (7.2– 8.6) \pm 0.23	5.4	I
1	10	7.8 (7.4– 8.3) \pm 0.18	3.6	I
3	3	7.3 (7.2– 7.5) \pm 0.18	2.1	I
Females				
6	25	7.8 (7.2– 8.2) \pm 0.13	4.2	I
2	29	7.7 (7.3– 8.3) \pm 0.09	3.1	I
9	6	7.6 (7.3– 8.1) \pm 0.24	3.9	I I
7	15	7.5 (7.0– 8.0) \pm 0.16	4.0	I I
1	13	7.4 (7.1– 7.8) \pm 0.10	2.6	I

samples 1 and 3 always comprise one of the distinct subsets. Samples form two subsets, which overlap at sample 2, in length of hind foot. Samples 2, 6, and 7 are never completely divided from each other into distinct subsets except for breadth across maxillaries, in which sample 6 is a distinct subset.

For females, sample 1 averaged the smallest in size for all measurements except squamosal breadth. In five measurements (condylobasal length, basal length, palatal length, length of nasals, and diastema), sample 1 is significantly different from all other samples. Individuals from sample 9 generally averaged among the smallest, and these were the smallest in squamosal breadth. Together with sample 1 this sample forms a distinct subset in greatest length of skull, palatofrontal depth, zygomatic breadth, mastoid breadth, and rostral breadth. In all cases, sample 9 fell into two subsets for these measurements. Either sample 6 or sample 7 had on the average the largest females for the species. Individuals in sample 7 were significantly larger than all others in five measurements (condylobasal length, basal length, palatal length, diastema, and zygomatic breadth), but individuals in sample 6 never averaged significantly larger than all others. It appears that samples of female *G. arenarius* fall into two size groups—large size (samples 2, 6, 7, 9) and small size (sample 1). Overlap in size of the groups is mainly exhibited by sample 9.

Multivariate analyses.—All nine samples for females and seven samples for males (no adult males were available from samples 5 and 8) were used in multivariate analyses of geographic variation in *Geomys arenarius*. Distance phenograms for males and females generated with

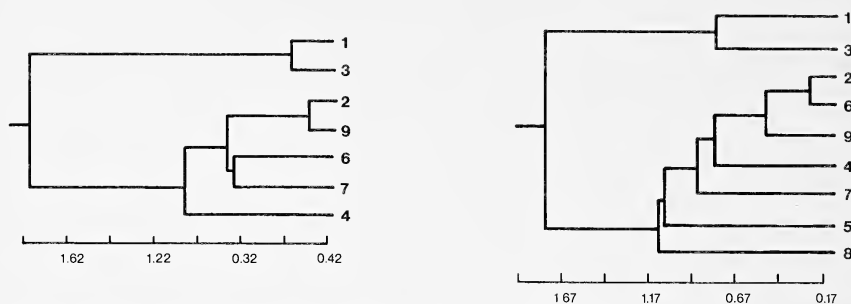


Fig. 2.—Phenograms of numbered samples (see Fig. 1 and text) of *Geomys arenarius* (males left, females right) computed from distance matrices and clustered by unweighted pair-group method using arithmetic averages (UPGMA). The cophenetic correlation coefficient for the phenogram for males is 0.899 and for females is 0.862.

the NT-SYS program package are illustrated in Fig. 2. The distance phenograms for males (cophenetic correlation value, 0.899) and females (cophenetic correlation value, 0.862) show the same basic patterns. Two major clusters are present. The upper cluster in both phenograms is composed of the samples from the vicinities of White Sand National Monument and Kenzin, New Mexico (samples 1 and 3), and the lower contains the remaining samples. Within the lower cluster, samples from the vicinity of Las Cruces, New Mexico (2), and vicinity of Fort Hancock, Texas (9), were the most closely related. The single male from sample 4 was the most distinct within this cluster. In females, the samples from the vicinities of Las Cruces, New Mexico (2), and El Paso, Texas (6) were the most similar within the lower cluster. The remaining samples form a graded series becoming increasingly distinct from samples 2 and 6 (samples 9, 4, 7, 5, and 8, respectively).

The first three principal components extracted from the matrix of correlation among characters are shown for males and females in Fig. 3. The amounts of phenetic variation explained by the first three principal components, for males and females, respectively, were 75.8 and 69.3 for component I, 12.7 and 11.5 for component II, and 6.0 and 10.1 for component III. Results of principal components analyses showing the influence of each character for the first three components are given in Table 3.

Most characters are heavily weighted in the first factor for both sexes. However, rather low values were found for length of tail, interorbital breadth, and breadth across maxillaries for males. In component II, characters with heavy weighting in males were length of tail, squamosal breadth, interorbital breadth, and breadth across maxillaries, and for females were length of tail and interorbital constriction.

Table 3.—Factor matrix from correlation among 16 characters of *Geomys arenarius* studied.

Characters	Males			Females		
	Component I	Component II	Component III	Component I	Component II	Component III
Total length	0.898	-0.252	0.241	0.829	-0.399	0.018
Length of tail	0.542	-0.735	0.106	0.330	-0.747	-0.423
Length of hind foot	0.946	0.065	0.243	0.745	-0.379	0.455
Greatest length of skull	0.993	-0.012	0.091	0.950	-0.175	0.216
Condylobasal length	0.993	-0.001	0.093	0.962	-0.164	0.119
Basal length	0.996	0.054	0.049	0.976	-0.045	0.121
Palatal length	0.933	0.086	0.022	0.951	0.041	0.158
Palatofrontal depth	0.971	0.181	0.050	0.971	0.194	-0.003
Length of nasals	0.967	0.091	-0.104	0.917	-0.178	0.189
Diastema	0.929	0.109	0.243	0.942	0.063	0.066
Zygomatic breadth	0.955	0.257	0.004	0.764	0.397	-0.460
Squamosal breadth	0.591	-0.723	-0.290	0.845	0.255	-0.383
Mastoid breadth	0.970	-0.044	-0.177	0.920	0.269	-0.257
Rostral breadth	0.843	0.419	-0.046	0.784	0.400	-0.362
Interorbital constriction	0.494	0.506	-0.673	0.314	-0.559	-0.566
Breadth across maxillaries	0.534	-0.576	-0.408	0.727	0.275	0.467

Interorbital constriction was the only character with high weighting in component III for males and females.

In both of the three-dimensional projections (Fig. 3), the small-sized samples from the vicinity of White Sands National Monument and Kenzin, New Mexico, are located to the left in the plots. They show a distinct separation from the other samples along component I. In males, samples 2 and 9 are closest to these samples, whereas in females samples 5 and 9 are closest. Sample 4 is located furthest to the right of the plot in males and samples 4 and 7 are furthest to the right in females, indicating that in overall size, individuals in these samples are the largest. We cannot detect any other major breaks in the variation among samples 2, 4–9 along the first component or the second and third components.

In both male and female *G. arenarius*, multivariate analysis of variance showed that there were significant ($P < .0001$) morphological differences among geographic samples in the following tests: Hotelling-Lawley's Trace; Pillai's Trace; Wilks' Criterion; Roy's Maximum Root Criterion.

Two-dimensional plots of the samples onto the first two canonical variates based on a matrix of variance-covariance among 13 cranial

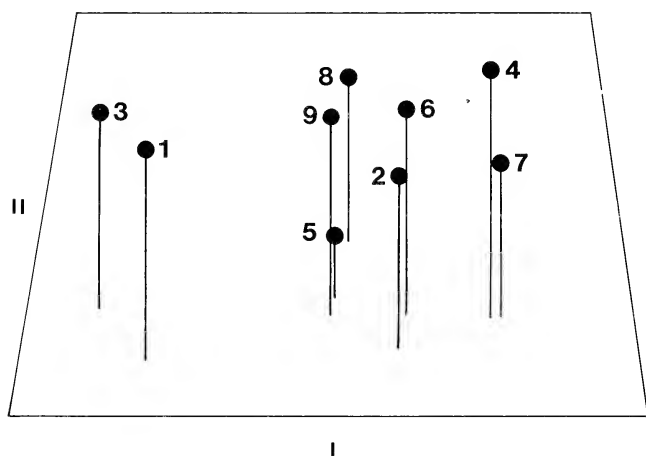
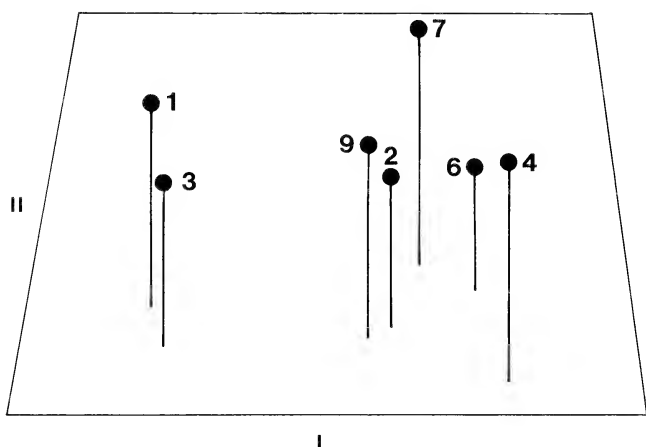


Fig. 3.—Three-dimensional projection of seven samples of male (upper) and nine samples of female (lower) *Geomys arenarius* onto the first three principal components based upon a matrix of correlation among 16 external and cranial measurements. Components I and II are indicated in the plots and component III is represented by height. See Fig. 1 and text for key to samples.

characters are presented for seven male samples in Fig. 4 and for nine female samples in Fig. 5. The percentages of phenetic variation represented in the first three canonical variates, males and females, respectively, were 45.04 and 46.96 for variate I, 27.07 and 23.71 for

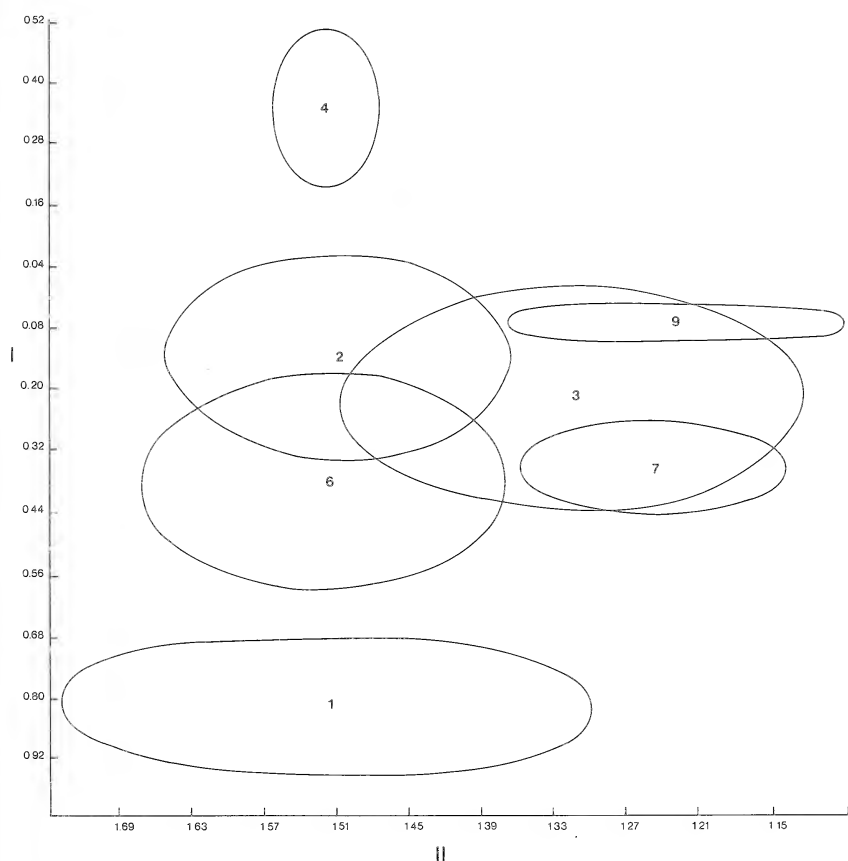


Fig. 4.—Two-dimensional projection of male samples (mean and one standard deviation) of *Geomys arenarius* onto the first two canonical variates based on a matrix of variance-covariance among 13 cranial measurements. See Fig. 1 and text for key to samples.

variate II, and 13.01 and 10.32 for variate III. The relative contribution of each character to the first three canonical variates in males and females are given in Table 4.

In both males and females, palatal length (males 16.2, females 22.03) contributed the heaviest toward separating the samples on the first variate. Other characters that contributed more than 10% on the first variate include condylobasal length, zygomatic breadth, and mastoid breadth for males and greatest length of skull, basal length, and palatofrontal depth for females. The following characters in males contributed more than 10% on the second variate, greatest length of skull, condylobasal length, basal length, and palatal length, and on the third

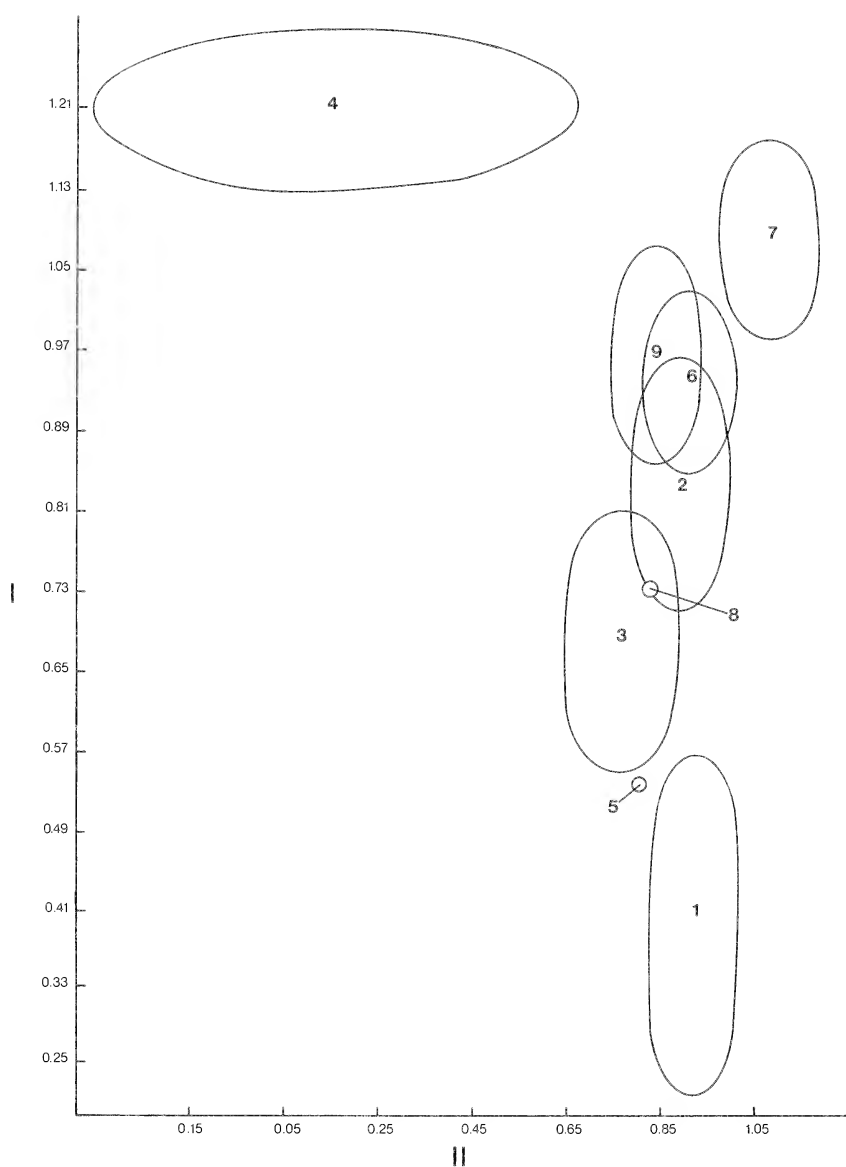


Fig. 5.—Two-dimensional projection of female samples (mean and one standard deviation) of *Geomys arenarius* onto the first two canonical variates based on a matrix of variance-covariance among 13 cranial measurements. See Fig. 1 and text for key to samples.

Table 4.—*Eigenvalues of canonical variates showing the percentage influence among 13 cranial characters of Geomys arenarius.*

Characters	Males					
	I		II		III	
	Normalized score	Percent influence	Normalized score	Percent influence	Normalized score	Percent influence
Greatest length of skull	0.07002704	6.35	-0.13295010	14.70	-0.01864911	1.32
Condylobasal length	-0.15596195	13.77	-0.11989710	12.90	-0.40425914	27.79
Basal length	-0.06744432	5.61	0.13533951	13.73	0.62722390	40.64
Palatal length	0.28522702	16.21	0.19105412	13.23	0.09435236	4.17
Palatofrontal depth	0.21062787	6.90	0.14557893	5.81	-0.10751664	2.74
Nasal length	0.09094108	2.96	0.14144744	5.61	0.26903025	6.82
Diastema	-0.31922869	9.75	-0.15928641	5.93	0.15683399	3.73
Zygomatic breadth	0.21777753	12.13	-0.04308363	2.92	-0.04995854	2.17
Mastoid breadth	-0.21474364	10.86	-0.03353211	2.07	0.13514711	5.32
Squamosal breadth	0.03319949	1.24	0.02034351	0.93	0.03680457	1.07
Rostral breadth	0.18962833	3.86	-0.35123820	8.71	0.03495951	0.55
Interorbital constriction	-0.14167600	1.81	0.18662330	3.06	0.24723997	2.46
Breadth across maxillaries	-0.54068301	8.55	0.53980533	10.40	-0.09921748	1.22

Characters	Females					
	I		II		III	
	Normalized score	Percent influence	Normalized score	Percent influence	Normalized score	Percent influence
Greatest length of skull	-0.09621047	17.05	-0.13456386	21.47	0.05660555	8.99
Condylobasal length	-0.03060782	5.29	0.17127426	26.63	-0.18111032	28.02
Basal length	0.12900585	20.93	0.03738308	5.46	0.10367251	15.07
Palatal length	0.19954883	22.03	-0.01399356	1.39	-0.12656545	12.52
Palatofrontal depth	-0.22064436	14.37	0.01464821	0.86	0.15197624	8.87
Nasal length	0.10353621	6.49	-0.12706368	7.17	-0.02466773	1.38
Diastema	-0.00887428	0.52	0.05728932	3.00	-0.02089690	1.09
Zygomatic breadth	-0.02705509	2.87	0.03618430	3.46	0.07753598	7.37
Mastoid breadth	-0.04863543	4.82	-0.09956718	8.89	0.05476377	4.87
Squamosal breadth	-0.02060481	1.56	0.12561332	8.59	0.05899616	4.01
Rostral breadth	0.05797401	2.32	-0.18096143	6.53	0.08977009	3.22
Interorbital constriction	-0.02595707	0.68	-0.12062981	2.87	-0.12885770	3.04
Breadth across maxillaries	-0.03363756	1.07	0.12973133	3.68	-0.05486456	1.55

variate, condylbasal length and basal length. The following characters in females contributed more than 10% on the second variate, greatest length of skull and condylbasal length, and on the third variate, condylbasal length and palatal length.

Examination of the two-dimensional plots for males and females (Figs. 4, 5) reveals the samples to be divided into three groups. At the bottom of both plots is the sample from White Sands (1). Individuals from this area are clearly the smallest in size for the species. Sample 4 is isolated at the top of each plot; these are the largest individuals of the species. The remaining samples are grouped at the center of each plot. Note that the standard deviation of males from sample 3 broadly overlaps with that of samples 2, 6, 7, and 9. In females, a different pattern is noted. Those samples to the west of the Rio Grande Valley—3, 5, and 8—fall at the lower end of variation for this central group. The one specimen from Samalayuca, Chihuahua (8), falls at the edge of one standard deviation for sample 2. The standard deviation for sample 3 overlaps that of sample 2 but the means for each sample lie outside the standard deviation. The one specimen from Columbus, New Mexico, lies between the standard deviations of samples 1 and 3.

Taxonomic conclusions.—Those individuals occurring along the floodplain of the Rio Grande River in Doña Ana Co., New Mexico, El Paso and Hudspeth cos., Texas, and adjacent Chihuahua, form a unified group characterized by large size. Those from the vicinity of Anthony, Chamberino, and Strauss (4) are among the largest and separate from other samples in some analyses. However, they seem best considered as one extreme in variation in this population. This group includes the holotype of the nominate subspecies from El Paso, El Paso Co., Texas, so the name *Geomys arenarius arenarius* should be applied to it.

The specimens from the vicinity of White Sands, Otero Co., New Mexico (1), are uniformly small in size. These specimens are geographically isolated from those along the Rio Grande River and we recognize them as a distinct subspecies, *Geomys arenarius brevirostris*, with the type locality of 9 mi W Tularosa, Otero Co., New Mexico.

This leaves the status of specimens from samples 3 (vicinity of Kenzin, New Mexico), 5 (near Columbus, New Mexico), and 8 (near Samalayuca, Chihuahua) undetermined. The individuals from sample 3 were as small as those from the White Sands area (1) in a number of characters. In some of the multivariate analyses, sample 3 grouped with sample 1, but in the SAS analyses, where characters were weighted, the specimens from sample 3 grouped closer to those samples from the Rio Grande. The single individuals from samples 5 and 8 grouped with the samples from along the Rio Grande in the cluster and principal component analyses. The position of sample 5 is less clear in the SAS analysis. Because the sample sizes for these areas are quite small and the bulk of the analyses, although inconclusive, seems to ally these samples with those samples from along the Rio Grande. These samples

may represent a third subspecies but status is certainly not as distinct as the other two groups and they are assigned to *G. a. arenarius* for the present.

***Geomys arenarius arenarius* Merriam, 1895**

Geomys arenarius Merriam, N. Amer. Fauna, 8:139, 31 January 1895.

Holotype.—Subadult male, skin and skull, USNM 18117/25015, from El Paso, El Paso Co., Texas; obtained on 13 December 1889 by Vernon Bailey, original no. 798.

Measurements of holotype.—Total length, 258; length of tail, 88; length of hind foot, 33; greatest length of skull —; condylobasal length, 42.9; basal length, 40.4; palatal length, 27.4; palatofrontal depth, 15.6; length of nasals, —; diastema, 14.6; zygomatic breadth, 27.0; mastoid breadth, 23.5; squamosal breadth, 18.4; rostral breadth, 9.4; interorbital breadth, 6.8; breadth across maxillaries, 8.1.

Distribution.—Occurring along the Rio Grande River in Hudspeth and El Paso cos., Texas, Doña Ana and Luna cos., New Mexico, and adjacent Chihuahua. The southernmost locality is 1.5 mi NE Porvenir (=Porvenir, Price and Emerson, 1971), Chihuahua (Anderson, 1972), and the northernmost is 7.6 mi N, 3.9 mi W Las Cruces, Doña Ana Co., New Mexico. The western edge of the geographic range is defined by the localities 8 mi S Samalayuca, Chihuahua, 2 mi S, 13 mi E Columbus, and Deming, New Mexico (Fig. 6).

Remarks.—All authors (Merriam, 1895; Bailey, 1895, 1905, 1932; Williams and Baker, 1974; Findley et al., 1975) seem to agree that *G. a. arenarius* prefers loose soil occurring in cultivated areas or along riverbanks. Populations of the species are quite high in the Rio Grande Valley and become agricultural pests in alfalfa fields, orchards, and the banks of irrigation ditches. These areas along the river bottoms are surrounded by hard stony mesas and desert mountains. According to Bailey (1932), specimens from Deming were from "the mellow sand along the Rio Mimbres." The area of distribution of *G. arenarius* is defined as northern Chihuahua Biotic Province by Blair (1950).

Bailey (1905) reported a specimen from near Monahans, Texas, as a *G. arenarius*. We have examined extensive material from the vicinity of Monahans and Kermit, Texas (Baker and Genoways, 1975), and are convinced that these specimens are best assigned to *Geomys bursarius knoxjonesi* (see also Davis, 1940).

Findley et al. (1975) reported specimens from 5 mi S, 11.8 mi E San Antonio, Socorro Co., New Mexico, at the extreme northern end of the Jornada del Muerto as *G. arenarius*. Our initial examination of these 10 specimens (only three adults) led us to question their specific

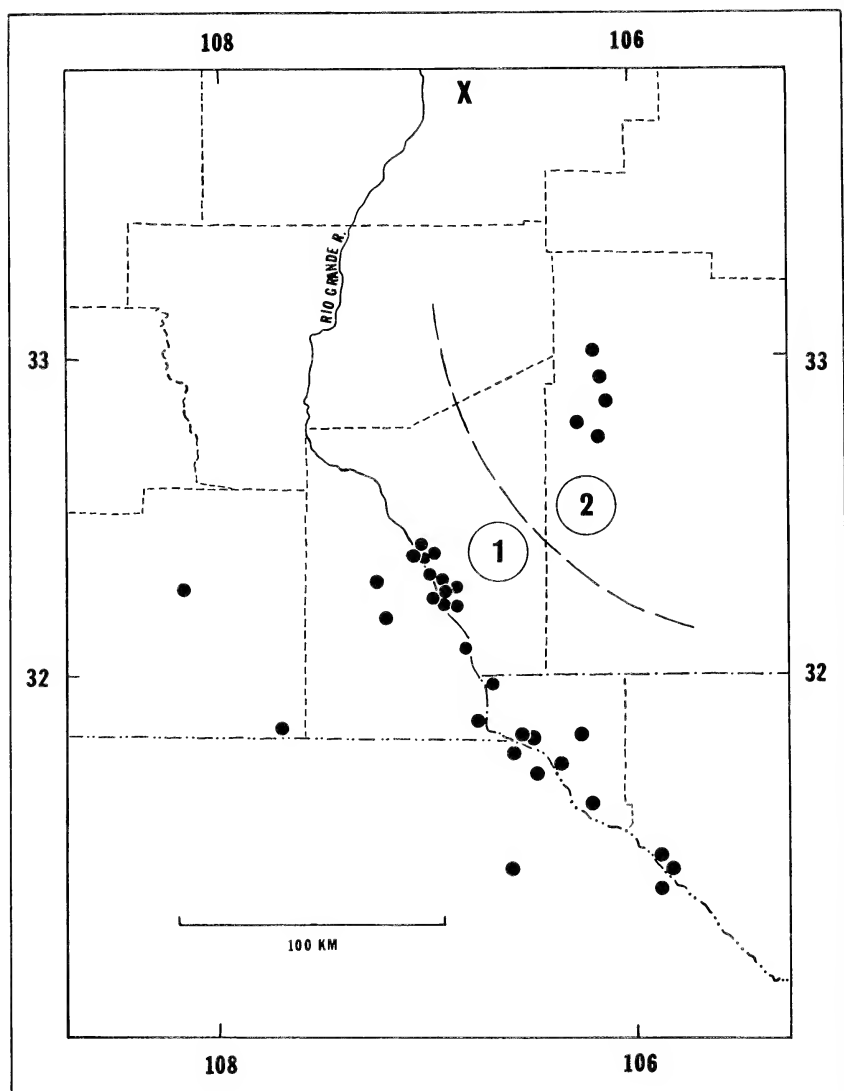


Fig. 6.—Geographic distribution of subspecies of *Geomys arenarius*: 1, *G. a. arenarius*; 2, *G. a. brevirostris*. "X" near top of figure is 5 mi S, 11.8 mi E San Antonio, Socorro Co., New Mexico, which is a locality for *Geomys bursarius knoxjonesi* discussed in text.

Table 5.—Discriminant function coefficients resulting from a discriminant function analysis comparing reference samples of *Geomys arenarius* and *G. bursarius*.

Characters	Discriminant function coefficients	
	Male	Female
Total length	-0.00175	—
Length of tail	0.00462	—
Length of hind foot	0.00387	—
Greatest length of skull	-0.00601	0.04494
Condylobasal length	-0.06442	-0.24073
Basal length	0.03102	0.02990
Palatal length	0.15608	0.33511
Palatofrontal depth	-0.05542	-0.10223
Length of nasals	0.02625	0.12173
Diastema	0.01615	-0.06087
Zygomatic breadth	-0.00102	-0.02849
Mastoid breadth	-0.02766	0.04680
Squamosal breadth	-0.08672	-0.06469
Rostral breadth	-0.18454	-0.12190
Interorbital constriction	0.26064	0.13909
Breadth of maxillaries	-0.07703	-0.06842
Length of basioccipital	—	0.04706

identity and to submit them to a discriminant function analysis to aid in their identification. Table 5 gives the discriminant function coefficients resulting from the comparison of reference samples of male and female *G. arenarius* and *G. bursarius*. The discriminant scores of male *arenarius* ranged from -0.471 to -0.813 and of *bursarius* -0.862 to -1.115. The one adult male from the vicinity of San Antonio (MSB 32641) received a discriminant score of -0.920 thus being classified as a *G. bursarius*. The range of discriminant scores for female *arenarius* was from 0.435 to 0.117 and *bursarius* 0.110 to -0.235. The two adult females from San Antonio (MSB 32600 and 32601) had scores of -0.098 and -0.067; both are identified as *G. bursarius*.

In a key to the pocket gophers of Texas, Davis (1940) used the width of the rostrum as compared to the length of the basioccipital to separate *Geomys arenarius* and *G. bursarius*. The rostral breadth is equal to or less than the basioccipital in *G. arenarius*, whereas in *G. bursarius* the reverse is true. For the three adults cited above and two subadults, the following values were found for these characters (rostral breadth is given first): MSB 32641, 10.2, 9.6; MSB 32600, 9.4, 9.1; MSB 32601, 9.4, 9.2; MSB 3266 (male), 9.6, 9.5; MSB 32834 (male), 9.8, 9.1. Thus all of these specimens, including the subadults, would key to *Geomys bursarius*. We conclude that the specimens from 5 mi S, 11.8 mi E San Antonio, Socorro Co., New Mexico, are best as-

signed to *Geomys bursarius knoxjonesi*. Based on available specimens and field investigation by us, it appears that the northern limit of the geographic range of *Geomys arenarius* is defined by the point that the Doña Ana Mountains meet the Rio Grande River. At this point, just north of Las Cruces, the river flows through a narrow channel along the western front of a series of low mountains. The narrow, gravelly channel does not provide suitable habitat for *Geomys* as well as several other species that show similar distributional patterns (see Findley et al., 1975; Williams, 1978). Evidently, *Geomys arenarius* has not entered the sandy areas of the Jornada del Muerto to the north and east of its geographic range.

Specimens examined (443).—CHIHUAHUA: Cd. Juarez, 3 (USNM); 7 mi SE Cd. Juarez, 5 (KU); 1½ mi NE Porvenir, 2 (KU); 8 mi S Samalayuca, 1 (KU). NEW MEXICO: Doña Ana Co.: 1 mi NE Aden Crater, 1 (MALB); Aden Crater, 2 (MALB); Lava flow, Johnson Ranch (31 mi NW El Paso), 1 (MSB); 5 mi N, 2 mi E Afton, 2 (UIMNH); 3.4 mi N, 3.2 mi W Afton, 4260 ft, T25S, R2W, Sec 24, 2 (NMSU); 3 mi N Afton, 2 (UIMNH); 2.5 mi N, 4.3 mi W Afton, 4240 ft, T25S, R2W, Sec 26, 1 (NMSU); 7½ mi W Bishop Cap Peak, 3825 ft, T24S, R2E, Sec 22, 1 (NMSU); 2 mi N, 1½ mi W Chamberino, 1 (UIMNH); 1½ mi N, 1½ mi W Chamberino, 4 (UIMNH); Doña Ana, 1 (KU); Kenzin, 3 (2 UIMNH, 1 UMMZ); 0.8 mi S, 5.5 mi W Kenzin, 4400 ft, T25S, R3W, Sec 36, 1 (NMSU); 3 mi S, 16 mi W La Mesa, 4350 ft, 2 (NMSU); 7.6 mi N, 3.9 mi W Las Cruces, 4000 ft, T22S, R1E, Sec 4, 1 (NMSU); 7.3 mi N, 3.9 mi W Las Cruces, 3935 ft, T22S, R1E, Sec 4, 2 (NMSU); 7.2 mi N, 3.4 mi W Las Cruces, 4000 ft, T22S, R1E, Sec 9, 1 (NMSU); 6.9 mi N, 3.6 mi W Las Cruces, 4000 ft, T22S, R1E, Sec 9, 1 (NMSU); 6.8 mi N, 3.9 mi W Las Cruces, 4000 ft, T22S, R1E, Sec 9, 1 (NMSU); 6.8 mi N, 3.5 mi W Las Cruces, 3935 ft, T22S, R1E, Sec 9, 1 (NMSU); 6.6 mi N, 3.7 mi W Las Cruces, 4000 ft, T22S, R1E, Sec 16, 1 (NMSU); 6.3 mi N, 3.7 mi W Las Cruces, 4000 ft, T22S, R1E, Sec 16, 1 (NMSU); 6.1 mi N, 3.5 mi W Las Cruces, 4000 ft, T22S, R1E, Sec 16, 1 (NMSU); 5.8 mi N, 4.1 mi W Las Cruces, 3930 ft, T22S, R1E, Sec 16, 2 (NMSU); 5.5 mi N, 5.1 mi W Las Cruces, 3940 ft, T22S, R1E, Sec 17, 3 (NMSU); 5.5 mi N, 4.0 mi W Las Cruces, 3930 ft, T22S, R1E, Sec 16, 1 (NMSU); 5.3 mi N, 5.2 mi W Las Cruces, 3940 ft, T22S, R1E, Sec 17, 1 (NMSU); 4.9 mi N, 5.0 mi W Las Cruces, 3935 ft, T22S, R1E, Sec 20, 4 (NMSU); 4.9 mi N, 3.6 mi W Las Cruces, 3920 ft, T22S, R1E, Sec 21, 3 (NMSU); 4.7 mi N, 4.8 mi W Las Cruces, 3920 ft, T22S, R1E, Sec 20, 1 (NMSU); 4.7 mi N, 3.0 mi W Las Cruces, 3920 ft, T22S, R1E, Sec 12, 1 (NMSU); 4.6 mi N, 4.8 mi W Las Cruces, T22S, R1E, Sec 20, 1 (NMSU); 4.4 mi N, 3.3 mi W Las Cruces, 3915 ft, T22S, R1E, Sec 22, 1 (NMSU); 4.0 mi N, 3.7 mi W Las Cruces, 3940 ft, T22S, R1E, Sec 28, 1 (NMSU); 4.0 mi N, 3.1 mi W Las Cruces, 3916 ft, T22S, R1E, Sec 27, 1 (NMSU); 2 mi N, 1 mi W Las Cruces, 2 (TNHC); 1.6 mi N, 3.0 mi W Las Cruces, T23S, R1E, 3 (NMSU); 1.5 mi N, 4 mi W Las Cruces, 3 (NMSU); 1 mi N, ¼ mi W Las Cruces, 2 (NMSU); 1½ mi NW Las Cruces, 3 (NMSU); NE Las Cruces, 3925 ft, T23S, R2E, 1 (NMSU); 15 mi W Las Cruces, 6 (LACM); W Las Cruces (E bank Rio Grande R.), 34 (TTU); 1½ mi S US 70-80 Rio Grande Bridge, 2 (MSB); Levee Rd, 3882 ft, T23S, R1E, Sec 27, 2 (NMSU); Las Cruces, 12 (1 MSB, 3 NMSU, 8 USNM); 1.6 mi S, 2.8 mi W Las Cruces, T23S, R1E, Sec 22, 6 (NMSU); 2 mi S, 3 mi E Las Cruces, 3900 ft, 1 (NMSU); 3.1 mi S, 2.8 mi W Las Cruces, 3880 ft, T23S, R1E, Sec 34, 4 (NMSU); NMSU Horticulture Farm, T24S, R2E, 1 (NMSU); 6.2 mi S, 2.4 mi W Las Cruces, 3850 ft, T24S, R1E, 1 (NMSU); 1.6 mi N, 1.5 mi W Mesilla, 3800 ft, T23S, R1E, Sec 22, 3 (NMSU); 1.2 mi N, 1.5 mi W Mesilla, 3800 ft, T23S, R1E, Sec 22, 3 (NMSU); 0.5 mi N, 2 mi W Mesilla, 3990 ft, 1 (NMSU); 0.3 mi S Mesilla, 1 (TNHC); 0.5 mi S,

2.0 mi W Mesilla, 3885 ft, 1 (NMSU); 0.5 mi S, 1.9 mi W Mesilla, 3885 ft, T23S, R1E, Sec 34, 5 (NMSU); 1.4 mi S Mesilla, 3905 ft, T25S, R1E, Sec 15, 2 (NMSU); 3.1 mi S Mesilla, T24S, R1E, Sec 11, 1 (NMSU); 4 mi S Mesilla, 1 (NMSU); 6.0 mi N Mesilla Dam, 1 (TNHC); 2.5 mi N Mesilla Dam, 1 (TNHC); 2.4 mi N Mesilla Dam, 1 (TNHC); 1.3 mi N Mesilla Dam, 1 (TNHC); 1.1 mi N Mesilla Dam, 4 (TNHC); 1.0 mi N Mesilla Dam, 5 (TNHC); 0.9 mi N Mesilla Dam, 4 (TNHC); 0.8 mi N Mesilla Dam, 2 (TNHC); 0.7 mi N Mesilla Dam, 3 (TNHC); 0.5 mi N Mesilla Dam, 1 (TNHC); 0.4 mi N Mesilla Dam, 1 (TNHC); 0.25 mi N, 0.125 mi W Mesilla Dam, 3990 ft, T24S, R1E, Sec 8, 2 (NMSU); ¼ mi N Mesilla Dam, 3905 ft, T25S, R1E, Sec 11, 1 (NMSU); 0.2 mi N Mesilla Dam, 3900 ft, T24S, R2E, Sec 7, 1 (NMSU); 200 yds N Mesilla Dam, T24S, R1E, Sec 12, 3 (NMSU); 12.3 mi W Mesilla Dam, 4260 ft, T24S, R1W, Sec 31, 4 (NMSU); 0.3 mi S Mesilla Dam, 1 (TNHC); 1.4 mi S Mesilla Dam, 3905 ft, T25S, R1E, Sec 15, 2 (NMSU); 1 ¾ mi S, 2¼ mi W Mesilla Dam, 3857 ft, T23S, R2E, Sec 17, 2 (NMSU); 3½ mi S, ¼ mi W Mesilla Park, 6 (MSB); 5 mi E Strauss, 1 (TCWC); ca. ½ mi N Anapra Bridge, Rio Grande floodplain, 1 (MALB); W bank Rio Grande at intersection with Country Club Rd, (NW El Paso), 1 (MALB); ¼ mi S Country Club Rd., 4 (MALB). *Luna Co.*: 2 mi S, 13 mi E Columbus, 1 (MSB); Deming, 3 (USNM); Mexican Boundary Line, Lat. 31°47', Long. 30°51', 7 (USNM). *TEXAS: El Paso Co.*: S on W Levee Rd., 1.2 mi from Fm. Rd. 1905 W of Anthony, 3 (MALB); 0.5 mi N, 0.15 mi W Canutillo, 1 (MALB); Canutillo (near river), 1 (MALB); 15 mi above El Paso (bank of Rio Grande), 2 (MVZ); 0.6 mi W Levee Rd. from Borderland Ave., 0.1 mi W Doniphan Dr. (El Paso), 2 (MALB); 1.5 mi W on Country Club Rd. N on Levee Rd. along Rio Grande for 0.3 mi (El Paso), 1 (MALB); down Country Club Rd. to Rio Grande River then N for 0.5 mi, 1 (MALB); Upper Valley, El Paso, 1 (TTU); 428 Lindbergh Ave., Upper Valley, El Paso, 1 (MALB); River Bend Farm, ½ mi S Sunset Dr., 1 (MALB); 2.5 mi S Country Club Rd., El Paso, 1 (MALB); NW El Paso, 1 (MALB); 3 mi N, 3 mi W Rio Grande R. Shore, El Paso, 1 (KU); El Paso, 21 (8 MALB, 1 UMMZ, 12 USNM); El Paso Zoo, 1 (USNM); E El Paso, 20 (USNM); 2 mi E city limits El Paso, 15 (MVZ); 30 mi E El Paso, 2.5 mi N Rio Grande (Fabens), 4 (TTU); 5 mi S, 8 mi E City Hall, El Paso, 3700 ft, 16 (KU); 10 mi SE City Hall, El Paso, 3700 ft, 17 (KU); 6.5 mi NE I-10 on Fabens-Carlsbad cutoff road, 1 (MALB); Fabens, 1 (USNM); 1 mi S Fabens, 50 (TTU); 2 mi S Fabens, 1 (MALB); 3 mi S Fabens, 1 (MALB); Horizon City, 2 (MALB); 1¼ mi N, ¾ mi W Ysleta, 21 (UIMNH); Ysleta, 2 (UIMNH). *Hudspeth Co.*: Ft. Hancock, 14 (2 AMNH, 10 KU, 2 USNM); 2 mi S Ft. Hancock, 7 (KU); 1 mi W McNary, 3 (UIMNH); McNary, 1 (UIMNH).

***Geomys arenarius brevirostris* Hall, 1932**

Geomys arenarius brevirostris Hall, Proc. Biol. Soc. Washington, 45:97, 21 June 1932.

Holotype.—Adult female, skin and skull, MVZ 50460, from E edge of [white] sand [9 mi W Tularosa], Tularosa–Hot Springs Road, Otero Co., New Mexico; obtained on 10 October 1931 by Annie M. Alexander, original no. 1174.

Distribution.—Confined to the White Sands area of Otero Co., New Mexico (Fig. 6).

Remarks.—Benson (1933) found *G. arenarius* to be most abundant about the edges of the ponds in the White Sands area. In many cases the burrows ran close to edge of the water and the earth thrown out in the mounds was saturated. Blair (1941, 1943) believed that *G. arenarius* was the most abundant mammal of White Sands, particularly

in the wet and dry valley associations of the interior. They were also found to be abundant in the grama grass-joint fir association of the periphery, but were rare in sumac-yucca association. Recent attempts by field teams from Texas Tech University to locate specimens of this taxon in the vicinity of Alamogordo and White Sands National Monument were unsuccessful. It is difficult to determine the status of this taxon because most of its former range is occupied by the White Sands National Monument and White Sands military installation; however, it clearly is not as abundant as indicated by Blair (1941, 1943). Specimens of *Pappogeomys castanops* were taken at several localities and it is entirely possible that this species is replacing *G. a. brevirostris* in many areas.

In contrast to most mammals living in the White Sands area, *G. a. brevirostris* is darker than other members of the species (Hall, 1932; Benson, 1933; Blair, 1941, 1943). Benson theorized that this dark coloration was the result of *G. a. brevirostris* living in areas of moist soil near ponds. Such soils tend to be darker than the dry sands of White Sands. Blair (1943) disregarded this theory because *brevirostris* is much darker than either the dry or wet gypsum of White Sands, and is darker than *G. a. arenarius*, which live in soils that are darker than the gypsum sand. He theorized that *G. a. brevirostris* was a recent invader of White Sands and that the dark color of this subspecies was fixed before it entered the area. The time since the invasion supposedly was too short to allow adaptation to the local conditions. Blair (1943) believed, and we agree, that the logical route of invasion followed by *brevirostris* was by way of the Escondida red sands, which extend southward from White Sands into Texas.

Our analyses reveal that individuals of the population from White Sands are uniformly small. They are approached in size by some individuals from west of the Rio Grande River but we do not believe there is any current relationship between these samples. Present data seem to indicate that *G. a. brevirostris* is isolated from *G. a. arenarius*. If the Escondida sands were the invasion route for *brevirostris*, then the intervening population no longer exists or else has not been located. However, much of this area is currently occupied by Fort Bliss.

Specimens examined (64).—NEW MEXICO: Otero Co.: 19 mi W Alamogordo, 1 (AMNH); 18 mi W Alamogordo, 18 (11 AMNH, 7 MSB); 12 mi W Alamogordo, 1 (MVZ); Alamogordo, 2 (UMMZ); 15 mi SW Alamogordo, 6 (LACM); 27 mi SW Alamogordo, 2 (UMMZ); 10 mi W Tularosa, 3 (UMMZ); White Sands, 10 mi SW Tularosa, 4100 ft, 5 (MVZ); sands SW Tularosa, 2 (MVZ); east edge sands, Tularosa-Hot Springs Rd., 11 (MVZ); 4 mi NW White Sands National Monument Museum, 2 (MVZ); White Sands National Monument, 8 (4 UIMNH, 4 UMMZ); interior White Sands, 3 (1 TNHC, 2 UMMZ).

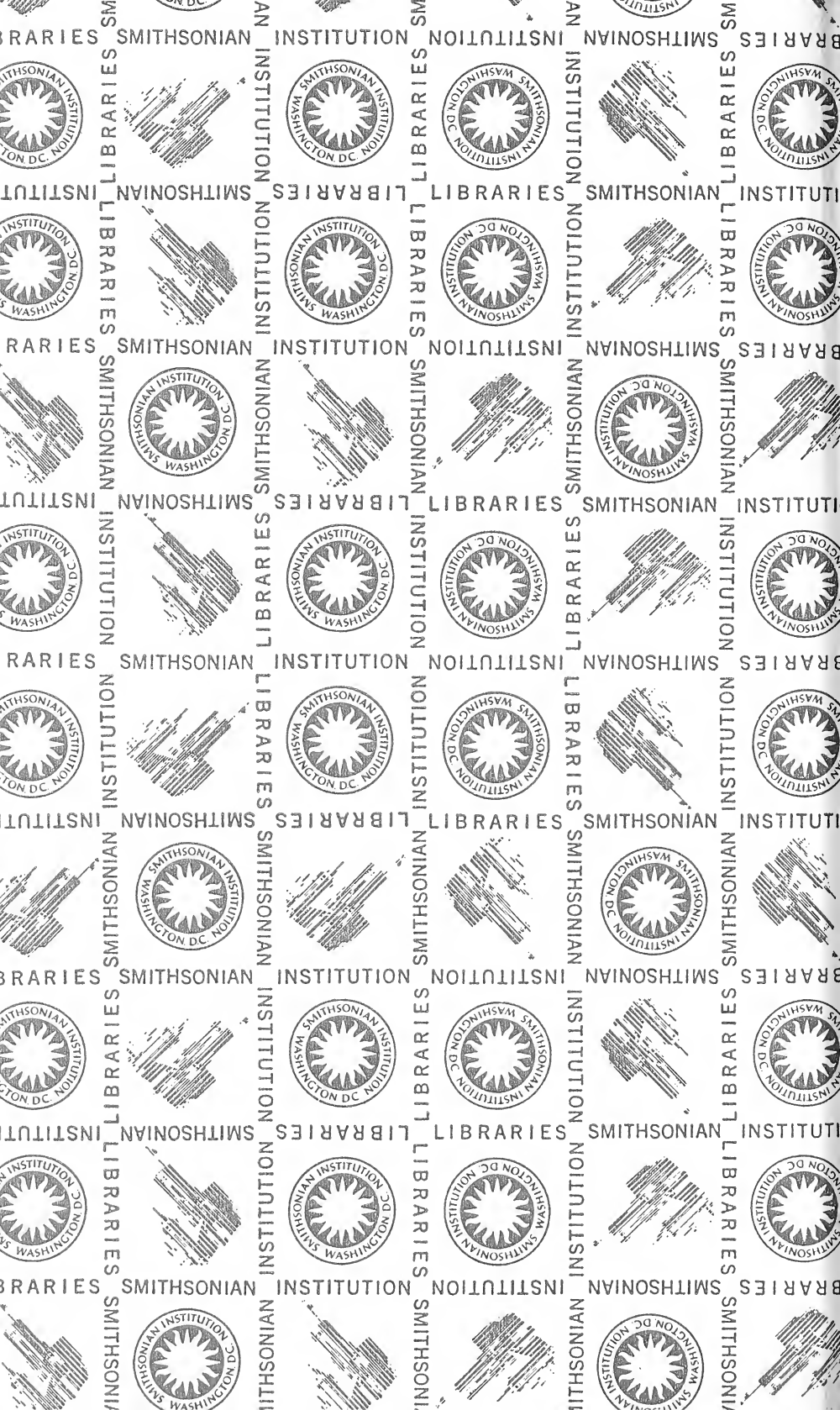
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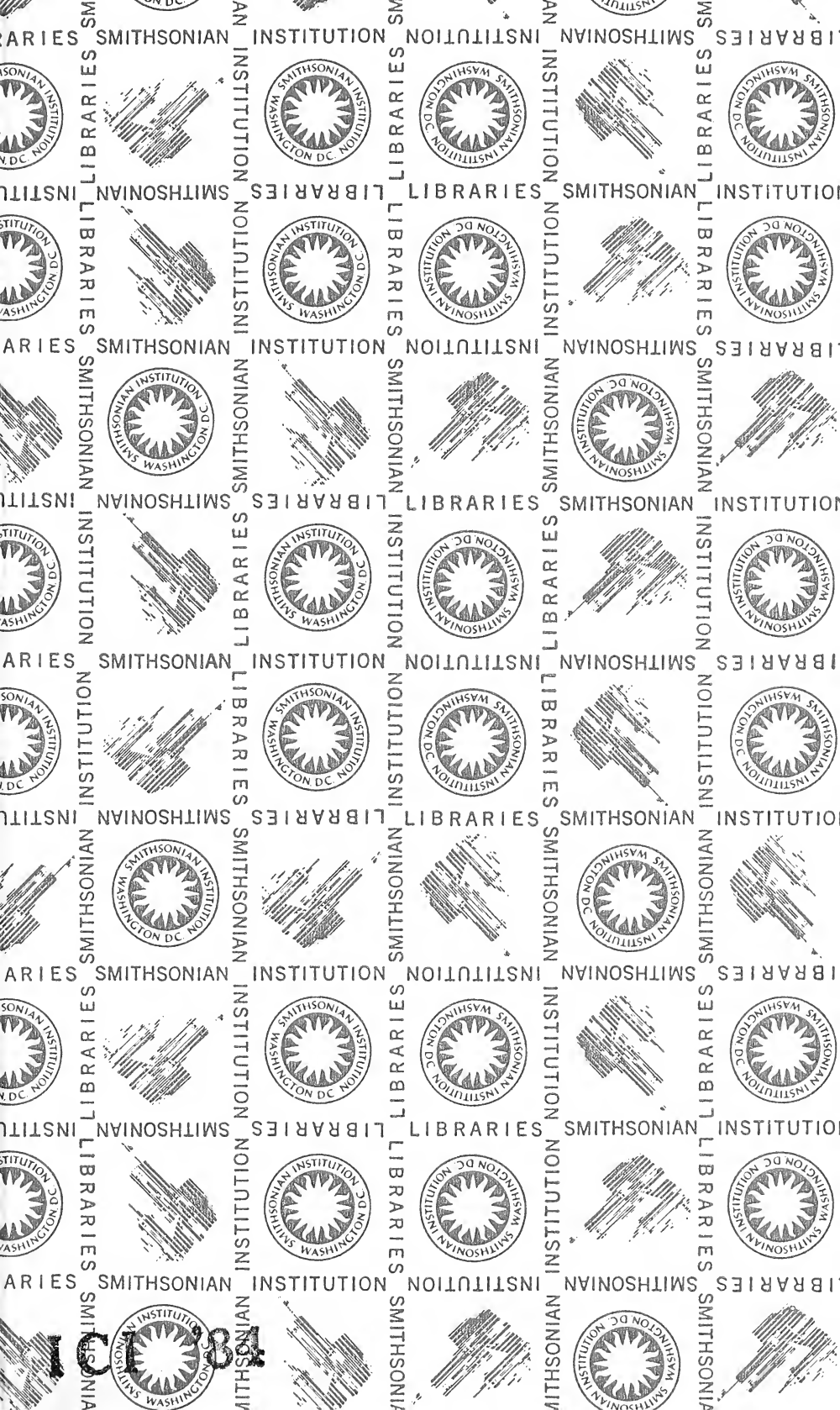
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